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Part 2

3.—Tropical spiny lobsters, *Panulirus* spp., of Western Australia (and the Indo-West Pacific)

by R. W. George *

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Abstract

Five species of spiny lobster *Panulirus penicillatus*, *P. versicolor*, *P. homarus*, *P. ornatus* and *P. polyphagus* inhabit waters of northwest Australia. The distributions of these and two other species *P. longipes* and *P. stimpsoni* all of which occur throughout the Indo-West Pacific region are described. Ecological separation of the widespread *Panulirus* species can be demonstrated and this results in regional dominance of one or other of the species depending upon local coastal conditions, particularly with respect to turbidity.

Introduction

In northern Australia, spiny lobsters are commonly referred to as "coral" or "green crayfish" in allusion to their supposed habitat and to the dominant colour of the common species *Panulirus versicolor*, *P. ornatus* and *P. homarus*. The two other species which occur in the general area are *P. penicillatus* which is brown and *P. polyphagus* which is blue-grey. None is restricted to live coral. Elsewhere in the Indo-West Pacific one or the other of these species supports a commercial fishery.

In an experimental fishing test in the Onslow region of Western Australia Mr B. K. Bowen (pers. comm.) set 15 Canadian and 6 Aden-type traps and he concluded that for *P. homarus* at least, the failure of the traps to take any spiny lobster was due to suspended clay and the surge of the tide. Diving and beach collections showed that four species occurred in the Onslow area. Apart from these observations by Mr B. K. Bowen and other reports by George & Holthuis (1965) and George (1966) which deal only with specimen descriptions or locality records, information on the abundance, habitat preferences or behaviour of the northern tropic Australian spiny lobsters is sparse.

This paper assembles existing published information on the ecology of these species around Australia and elsewhere, integrates this with personal observations, and proposes an explanation for their regional and local abundance.

I wish to acknowledge the opportunity afforded by F.A.O./U.N. to work in East Aden on *Panulirus homarus* (FAO/UN, 1963) and also that afforded by Ross Fisheries (Australia) Pty Ltd to study in the western Indian Ocean. My early observations on the northern coasts of Western Australia were carried out whilst employed by the C.S.I.R.O. Division of Fisher-

ies and Oceanography. I also wish to acknowledge the assistance of Dr G. M. Storr and Mr R. J. McKay of the Western Australian Museum for their critical discussion.

Key to tropic Indo-Pacific *Panulirus*, based on colour markings

1. Abdomen with transverse pale bands 2
Abdomen without pale bands 3
2. Legs striped; general colour dark green *P. versicolor*
Legs spotted; general colour grey-blue *P. polyphagus*
3. Abdomen with many very fine pale spots all over dorsal surface 4
Abdomen without small spots on dorsal surface; general colour green *P. ornatus*
Abdomen with moderate number of moderate sized spots; general colour red-brown *P. longipes*
4. Legs spotted or blotched; general colour light green or blue-green *P. homarus*
Legs striped 5
5. Side of abdomen with short white vertical line and conspicuous white spots on each segment; general colour drab *P. stimpsoni*
Side of abdomen uniformly spotted without white line or conspicuous spot on each segment; general colour brown or red *P. penicillatus*

Key to tropic Indo-Pacific *Panulirus*, based on morphological features

1. Each abdominal segment with a transverse groove 2
Abdominal segments without transverse grooves 4
2. Anterior margin of abdominal grooves scalloped *P. homarus*
Anterior margin of abdominal grooves not scalloped 3
3. Antennular plate with 4 equal principal spines fused at base *P. penicillatus*
Antennular plate with 2 principal spines and some smaller spines behind *P. longipes*
4. Flagellum of exopod of second maxilliped well-developed, multi-articulate *P. polyphagus*
Flagellum of exopod of second maxilliped small or absent 5
5. Male pleopod three times as long as wide; carapace not pubescent; abdomen smooth in adult, faint transverse pubescent areas in juveniles *P. versicolor*
Male pleopod twice as long as wide; carapace with faint pubescence; abdomen always smooth and naked *P. ornatus*
Male pleopod twice as long as wide; carapace with distinct pubescence; segments of abdomen with distinct sunken pubescent areas *P. stimpsoni*

* Western Australian Museum, Beaufort Street, Perth, W.A.

Geographic distribution

Five of the six known species from Australian tropic waters occur in Western Australia. All six are dealt with here since it may only be a matter of time before the sixth is recorded from Western Australia. These species occur elsewhere through the Indo-West Pacific region (of which tropical Australia is a part) and only one further spiny lobster, *Panulirus stimpsoni* Holthuis 1963 from Hong Kong and China, is known from this vast area. In other words, all but one Indo-West Pacific *Panulirus* species occur in Australian waters. Details of geographic distribution are set out in Table 1. This is based on Holthuis' basic revision (1946) supplemented by regional appreciations conducted by Barnard (1950) for Natal and East Africa; Charbonnier and Crosnier (1961) for Madagascar; Deshmukh (1964), Chhapgar and Deshmukh (1964) and Satyanarayana (1961) for west Indian coast; De Bruin (1962) for Ceylon; Naiyanetr (pers. comm.) for west Thailand; Kubo (1954) for Japan; Rapson (1962) for New Guinea; Holthuis and Villalobos (1962) and Holthuis and Loesch (1957) for East Pacific offshore islands.

Three species, *P. penicillatus*, *P. longipes* and *versicolor* are notable for their ability to inhabit, in moderate or quite high numbers, islands which are well away from the relatively continuous coastal waters of the Indian and West Pacific Oceans. *Panulirus penicillatus* has the greatest ability to disperse and colonise, occupying 240° of longitude from the western Red Sea (30° East) to the Galapagos Is (90° West). It is the only spiny lobster to cross the Pacific Oceanic Barrier recognised by Eckman (1953), and would be called by Briggs (1961) a Transpacific species. Neither *P. longipes* nor *P. versicolor* has crossed the Pacific Barrier or even colonised as far east as Hawaii. The success of their larvae is apparently restricted by distances greater than about 1000 miles.

The other three fairly widespread species *P. homarus*, *P. ornatus* and *P. polyphagus* are only very occasionally able to successfully establish

far from mainland coasts (e.g. the presence of *ornatus* at Mauritius) and are essentially coastal species. *Panulirus stimpsoni* has the most limited distribution and is included in Table 1 to complete the distribution picture for all known tropic species of *Panulirus* in the Indo-West Pacific region.

Ecological observations

De Bruin (1960 and 1962) has studied spiny lobsters in Ceylon for several years by diving and trapping. He has documented ecological and behavioural differences between some of the species and has provided the first indication that the localised dominance by a species in a given area is probably due to that species' ecological requirements being met by the particular environments available around Ceylon. His two publications serve as excellent basic studies for this paper. I have had the good fortune to dive with De Bruin on one of his nightly surveys; it was a very rewarding experience.

Panulirus penicillatus.

De Bruin (1962) found this species in small numbers on both east and west coasts of Ceylon and concluded that it occurs only in shallow waters subject to surf as exists on the rocky reef front. It is present in much larger numbers and is commercially exploited at Revillagigedo I. (Holthuis & Villalobos, 1962) and at Galapagos where it also prefers the shallow waters to 2 metres, displacing the east Pacific species *P. gracilis* from the shallow part of its normal range (Holthuis & Loesch, 1967).

In tropical Western Australia it is not abundant; moulted shells have been collected in low numbers along the beach inside the fringing reef which runs from Point Cloates to North West Cape. Presumably, the species lives out on the seaward reef edge. Commercial traps set for *P. cygnus* at Murchison River, Abrolhos and experimental surveys around

TABLE 1

Distribution of tropical Indo-West Pacific *Panulirus*
(0=no authentic record; +=relative abundance)

	penicillatus	longipes	versicolor	homarus	ornatus	polyphagus	stimpsoni
Natal	+	0	+	++	0	0	0
Madagascar	++	+	+	++	+	0	0
East Africa	+	+	+	+	+	0	0
Red Sea (proper)	++	0	0	0	++	0	0
South Arabian Coast	+	0	+	++	+	0	0
Indian Coast, West	+	0	+	++	+	0	0
Ceylon	+	+	++	+++	+	+++	0
Bay of Bengal	0	0	0	0	+	+	0
West Thailand	+	+	+	+	+	0	0
China Sea and East Indies	0	+	+	+	+	+	0
Japan and Formosa	+	+	+	+	+	+	Hong Kong
N. Australia	+	0	+	+	+	0	0
New Guinea	++	+	+	+	+	+	0
South-West Pacific	+	+	+	+	++	0	0
Central Pacific	+	0	+	0	+	0	0
Hawaii	+	0	0	0	0	0	0
E. Pacific offshore islands (Galapagos and Revillagigedo)	++++	0	0	0	0	0	0
Indian Ocean offshore islands	Mauritius	Mauritius	Cocos I	0	0	0	0
	Reunion	Reunion	Seychelles		Mauritius		
	Seychelles	Seychelles	Christmas I.				
	Chagos	Christmas I.					
	Christmas I.						
	Cocos I.						

Monte Bello Island have yielded very occasional specimens. Although the species will enter baited traps (see also Charbonnier and Crosnier 1961 and De Bruin 1962) it is commercially taken by hand at the Galapagos; it is fairly docile, and makes little attempt to back away into the normal retreats of spiny lobsters when approached by a gloved hand (Holthuis and Loesch, 1967). This has also been observed by R. J. McKay (pers. comm.) at Black Ledge off Onslow, W. Australia.

It is not necessarily restricted to coral reef, and in fact Charbonnier and Crosnier (1961) suggest that it occurs on the south coast of Madagascar because these rocky areas lack coral; one can also conclude that clear, non-turbid water conditions such as exist on oceanic islands are preferred conditions.

Panulirus longipes

De Bruin (1962) used the name *P. japonicus* for this species but George and Holthuis (1965) have shown that Ceylon specimens such as De Bruin figured are the spotted-leg form of *P. longipes*. The other form which has striped legs occurs mainly in the west Pacific and so far has not been found sympatric with the Indian Ocean spotted-leg form. This species has not yet been recorded from northern Australia but it occurs around this region at Christmas I., New Guinea and Heron I., Great Barrier Reef.

De Bruin (1962) found *P. longipes* on both coasts of Ceylon but nowhere in abundance. It preferred the seaward edge of the reef plateau at depths of 6-14 metres i.e. below the shallow range of *P. penicillatus*. Since I have collected *P. longipes* in very shallow water (1-2 metres depth) at Mauritius, Seychelles, and Heron I., Great Barrier Reef, it is possible that at Ceylon *P. longipes* (like *P. gracilis* at Galapagos) is displaced by *P. penicillatus* in shallow waters.

Although *P. longipes* enters traps it has not been commercially exploited to any extent anywhere in spite of its obvious nocturnal habits even on moonlight nights (De Bruin 1962). Substrate and temperature preferences are broad in this species since I have collected them in the shallow, very warm, coral reefs of Mauritius, Seychelles and Heron I., and they have also been taken in traps set on rocky bottom for *Jasus verreauxii* in the subtropic waters of southern Queensland at a depth of 130 metres (George & Holthuis 1965). Although its temperature and depth ranges are wide, it apparently prefers non-turbid waters as does *P. penicillatus*.

Panulirus versicolor

De Bruin (1962) found this species to be dominant on the east coast of Ceylon and to occur in depths greater than 6 metres. They are extremely gregarious but since they do not enter pots his assessment of their relative abundance had to be carried out by diving.

His conclusions are confirmed by personal observations except that in places such as Heron I. (Qld.), North West Cape, Thevenard and Lowendal Is. (Western Australia), East Aden, and Seychelles *P. versicolor* also occurs in shallow waters of less than 6 metres. Perhaps

at Ceylon, where all species occur in close proximity to one another, depth displacement of species is most obvious.

In northern Australia *P. versicolor* is probably the most common of all the tropic spiny lobsters (B. K. Bowen pers. comm.). Its adult habitat includes waters and substrates which contain some fine sediment (e.g. on the shallow reef flat at Thevenard I.) as well as substrates of prolific coral where the waters are very clear. Juveniles apparently prefer clearer rather than muddier conditions. At Lowendal I. and on the outer face of the fringing reef at Thevenard I. where there is constant movement of very clear water, many juveniles have been observed with their bodies neatly fitting into holes in the reef, leaving their long white antennae protruding.

Panulirus homarus

Gordon (1953) correctly regarded *P. homarus* as a morphologically variable species which includes forms previously named as *P. dasypus* and *P. burgeri*. The variability is most apparent in the degree of scalloping and the completeness of the abdominal grooves as well as the number of joints on the flagellum of the second maxilliped (De Bruin 1962). In Ceylon, De Bruin (1962) found that *P. homarus* was the most promising spiny lobster for exploitation since it was the most abundant, it enters baited traps, it occurs from shallowest reef front to the deepest fissures in granite (14 metres) and it is extremely gregarious.

In East Aden the above observations on behaviour and habitat were confirmed and it was concluded that it is promising for exploitation (FAO/UN 1963). That report mentioned that *P. homarus* also occurs on volcanic or limestone reefs and that the cooler, poor-coral coasts of East Aden which are influenced by upwelling in the Gulf of Aden are optimal for it. Heavy seas and flash floods occur during the monsoon and weed dislodges at the end of the monsoon season. This results in a seasonal alternation of cloudy, turbid conditions during the monsoon (June to September) and crystal clear conditions during the remainder of the year.

In northern Australia *P. homarus* is recorded from Broome and near Onslow on beaches and nearby islands. As noted by Mr B. K. Bowen (pers. comm.) the conditions here are always turbid to some degree due to the great rise and fall of tide in an area where wind-blown desert dust and irregular, summer-flowing rivers provide the fine sediments. Mr R. J. McKay (pers. comm.) reports that adults usually occur in clearer water than juveniles and the juveniles can be found in very muddy conditions. Just off the Onslow beach he pulled 2 inch specimens from close-fitting holes in dead coral heads by their very long, deep maroon antennae. It is possible that muddy water is necessary for the juveniles of *P. homarus* and that although the adults can tolerate occasional turbidity they prefer cooler, clearer water. These conditions occur at East Aden; the water temperature is lowered due to upwelling at the time of the monsoon and the turbid water condition can be due to either run off after flash floods or to disturbance of fine sand by heavy seas.

Panulirus ornatus

In Ceylon this species is dominant on the northern coast, lives singly or in pairs in shallow water, and its density can only be estimated by diving since it does not enter traps (De Bruin 1962). In Western Australia it has been collected from several localities near North West Cape, Thevenard I. near Onslow, Dampier Archipelago and Broome either by shallow diving near reefs or hand collecting on the reef flats and beaches (moulted shells).

Charbonnier and Crosnier (1961) suggest that *P. ornatus* prefers the corals of Madagascar but at Lamu on the East African coast where a hand fishery for *P. ornatus* operates, conditions are generally turbid and not good for coral growth. At Mauritius, I was told by divers that *P. ornatus* occurs inside the lagoon in the deeper channels that run from small rivers across to the outer edge of the fringing reef. Here the water conditions are certainly cloudy due to the fine coral sediment of the lagoon supplemented by some terrestrial detritus derived from the streams.

The specimens which were collected near North West Cape, Western Australia, were taken from their shelter beneath an oyster-covered rock off Melyering Beach; the water depth was about 2 metres and the whole of the bottom of the pool as well as the offshore reef surrounding it was covered with a very fine white sediment which was very easily stirred up by a diver's swim fins. *P. ornatus* appears not only to tolerate but to prefer areas subjected to regular or occasional turbid conditions.

Panulirus polyphagus

This species was only recorded once by De Bruin (1962) trawled on a sea bottom of mud on the north east coast of Ceylon. There are four specimens of *P. polyphagus* from northern Australian waters in the collection of the Western Australian Museum; these are from Broome, Derby, Joseph Bonaparte Gulf and Darwin.

P. polyphagus is the dominant species on the upper west coast of India; it is taken by hoop nets or by trawling to depths of at least 70 metres and constitutes 99% of the commercial catch (Deshmukh, 1964). Because *P. polyphagus* can be taken by traps or by trawl, its absence in quantities over most of the Indo-West Pacific zone can be regarded as real and it can be concluded that the preferred habitat for this species is typified by the muddy upper west coast of India.

Discussion

Ecological separation of the 6 sympatric species of the Indo-West Pacific region is indicated since regional or habitat dominance can be demonstrated. On the regional scale, *P. ornatus* is the dominant species in East Africa, *P. homarus* on the South Arabian coast, *P. polyphagus* on the Indian west coast and *P. penicillatus* on the east Pacific offshore islands. On a much smaller scale, personal observations at three localities in the North West Cape area of Western Australia have shown that on the limestone reef directly below the North West Cape Lighthouse, only *P. cygnus* (the dominant west coast and com-

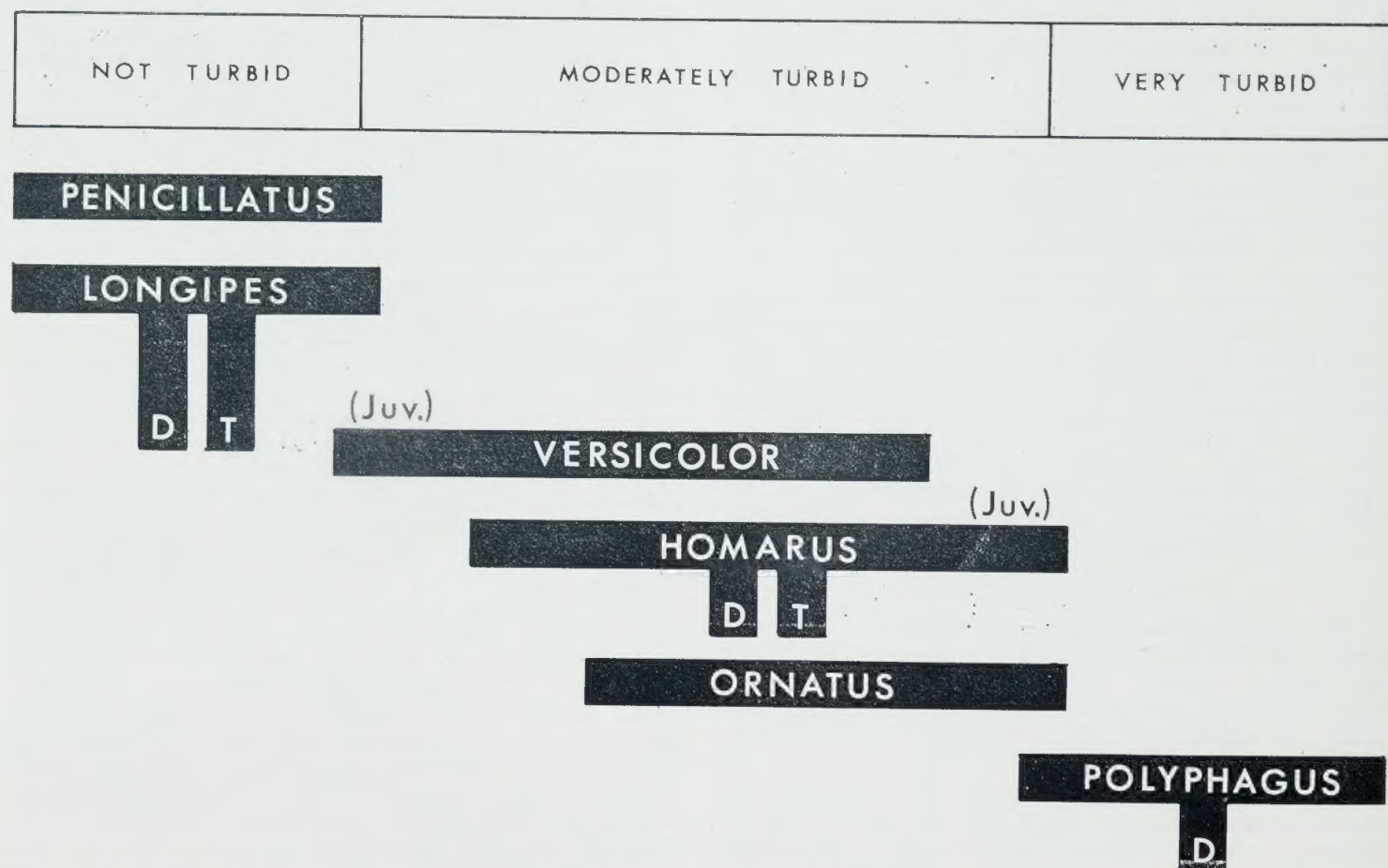


Figure 1.—Comparison of habitats occupied by tropical Indo-West Pacific *Panulirus* spp. with respect to turbidity, depth and temperature. D and T represent degree of habitat extension into deeper (D) and cooler (T) waters below the shallow tropic habitat, common to all six species.

mercially important spiny lobster) is found while 3 miles to the northeast among the coral at the North West Cape reef only *P. versicolor* occurs, and 20 miles southwest of the North West Cape Lighthouse, in the pool with fine sediment at Melyering Beach *P. ornatus* was the only species found.

A fullscale investigation would probably reveal numerous environmental factors which could lead to the observed ecological and habitat separation of these species. However, turbidity of the water, type of substrate, depth and temperature are the only ones that can be considered here because of the lack of data pertaining to other factors. For example, at least three other ecological factors (food, salinity and oxygen) should be considered, but our knowledge of the comparative requirements of these for any of the species is non-existent.

Figure 1 compares habitats occupied by the tropic spiny lobsters with respect to water turbidity, depth and temperature. Substrate has not been included since it can be modified by interaction of the three previously mentioned factors. For example "live coral" as a substrate can be abundant in regions of very low turbidity, high temperature and shallow depth but can be very sparse where any one of these factors is limiting. Also substrates of "mud" can be produced by entirely different processes; fine terrigenous sediment can be carried into the sea by river or wind or it can be produced by the breakdown of skeletons of marine organisms or by chemical processes. It is not possible at this stage to suggest whether spiny lobsters discriminate between these mud sources or not.

If Figure 1 does represent major ecological influences determining the occurrence and abundance of tropical spiny lobsters, then one would expect that the densities of each species would decrease as the limits of the "normal" geographic (or ecologic) range are approached. Some support is given to this expectation by the following observations.

On the eastern side of the Arabian Sea the degree of turbidity in the sea increases as one progresses from Galle, Ceylon, up the west coast of the Indian Peninsula. In the northern regions near Karachi and Bombay, the seasonal onshore monsoon results in heavy run-off of terrestrial sediment which replenishes the extensive mud areas at the coast; along the lower part of the Indian Peninsula, the amount of sediment carried into the sea is very much less because the rivers are short and run through the hard rocks of the Western Ghats. *P. penicillatus* which prefers clear water is in low density on the west coast of Ceylon (De Bruin, 1962) and has been recorded only once from India and then from the southern State of Kerala (Satyanarayana, 1961). *P. longipes* which also prefers clear waters occurs in low numbers in Ceylon but has never been recorded from India. *P. homarus* is the most abundant species on the west coast of Ceylon (De Bruin, 1962) and at Kerala State, India (Satyanarayana, 1961) and it extends in low numbers as far as Bombay (Deshmukh, 1964). *P. polyphagus* occurs rarely at Ceylon, but at Bombay and Karachi it predominates and is

taken commercially. Although *P. versicolor* and *P. ornatus* do occur along the Indian and Ceylonese west coasts, relative densities are difficult to assess. However on the east coast of Ceylon it is reasonable to suggest that *P. homarus* which dominates the north coast inhabits muddier conditions than the dominant *P. versicolor* on the mid-east coast (see De Bruin, 1962).

The relative abundance of spiny lobsters along the Indian and Ceylonese coasts warrants comparison with the situation along the north-west coast of Australia. Apart from the very muddy conditions in Exmouth Gulf and Nickol Bay, the region from North West Cape to Broome is slightly turbid compared with the region east of Broome which is very turbid. Many physical factors contribute to the amount of turbidity in the coastal waters of a particular region but the most direct contribution is by large rivers carrying high concentrations of sediments. This is exemplified in India by the Indus which discharges near Karachi and in the northwest of Australia by the river systems which discharge between Derby and Darwin. Where muddy river discharge is not dominant, a region may be characterised by wind-borne sediment (e.g. along the desert coast between Broome and Onslow where offshore winds occur) or by local *in situ* contributions of fine sediment of organic origin (e.g. in Shark Bay, Western Australia). The rise and fall in tide also appreciably affects turbidity where this is great such as along the northwest coast of Australia.

In the clear waters just to south of North West Cape *P. penicillatus* occurs, but it only extends to the east on offshore islands such as the Monte Bellos and at Black Ledge where clear conditions exist. *P. polyphagus* on the other hand has only been recorded in the eastern part from Broome to Darwin; its abundance would be better known when trawling operations commence on the muddy bottoms which hold promise of penaeid prawn fisheries.* In the region of moderate turbidity between Onslow and Broome *P. ornatus* and *P. homarus* occur fairly close to the coast whereas *P. versicolor* prefers the clearer areas further offshore. One unexpected absentee from the North West Cape region is *P. longipes*. It has good dispersal powers, tolerates subtropical temperatures and prefers clear waters such as exist south of North West Cape. Perhaps its place is taken on the subtropic west coast by the dominant *P. cygnus* whose ecological ranges and preferences appear to be very similar to the subtropic part of the *P. longipes* range.

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* Note added in press. Recently exploratory prawn trawling by the Department of Fisheries and Fauna in the region between Admiralty Gulf and the western side of Joseph Bonaparte Gulf has shown that the only species of *Panulirus* trawled was *P. polyphagus*; about 20 specimens were taken in the prawn nets in April 1968.

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4.—Drought effects in the Gibson Desert

by J. S. Beard*

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Abstract

On a recent expedition through part of the Gibson Desert and adjacent areas it was observed that most of the vegetation had been severely affected by drought during some recent period, with widespread death and dieback. Regeneration had since taken place. Brief details of the principal vegetation types and of the effects of drought are given. The latter are shown not to have been caused by fire and are traced to three years of drought in 1961-4. It is suggested that infrequent severe droughts cause cyclic death and regeneration of vegetation in these arid areas, producing more or less even-aged stands.

Introduction

In September-October 1966 a party consisting of the writer and Mr A. S. George, a botanist on the staff of the West Australian Department of Agriculture, travelled across the southern part of the Gibson Desert and through the mountainous area of the Warburton, Rawlinson and adjoining ranges (the Warburton Natural Region of Clarke, 1927) subsequently crossing the Great Victoria Desert in a southerly direction. This whole region, lying between the 123rd meridian and the State boundary at the 129th meridian, and south of the 24th parallel, was until recently one of the most inaccessible parts of Australia, but between 1956 and 1963 was opened up by numerous graded tracks constructed by the Commonwealth Government for survey purposes (Beadell, 1965). These tracks were used by our party for observations of flora and vegetation and it was soon noticed that much of the plant cover was in process of regeneration after a period of severe drought which must have occurred in recent years. Particular note was therefore taken of drought effects, and on return rainfall records were obtained for a climatic analysis, forming the subject of this paper.

General description of the region

The most varied and scenically interesting country occurs in the east of the region where mountainous country typical of Central Australia crosses the State boundary for some distance. In latitude 25° the Petermann Ranges and their continuation as the Schwerin Mural Crescent and Rawlinson Range extend westward for 90 miles, with a group of minor ranges to the north of them. These are low mountains of massive quartzite with flat, sandy plains between them, usually with dunes. Further south, in latitude 26° another chain of small isolated mountains of gneiss much intruded with basalt and basic dykes extends 150 miles westward

from the State boundary to end at the Warburton Range. The country adjoining these ranges consists mainly of plains of heavy soil under mulga, though sandy areas do occur.

To the west and south of this massif of ancient rocks the country is underlain by more or less horizontal sediments of Permian and later ages, predominantly sandstones, and is of relatively low relief. Broad, level plateaux are dissected by shallow valleys often bordered with low breakaways. Immediately to the west of the mountain range complex this plateaux country consists predominantly of very extensive surfaces of ironstone gravel with limited sandy valleys in which dunes are developed. This area constitutes the Gibson Desert and in the region studied (south of the 24th parallel) it occupies a triangle whose sides bear 20° and 315° respectively from an apex at lat. 27° 30' S, long. 126° E. Laterite plains, with a characteristic vegetation, are confined within this triangle. Outside it, the country is predominantly sandy with belts of dunes interspersed with heavier soil flats. Further to the southwest, sand plains without dunes are encountered. The sandy country outside the triangle may be said to constitute the Great Victoria Desert. The most conspicuous effects of drought were observed in the Gibson Desert and mountain area and diminished south of the 27th parallel.

Human settlement in this region consists of the United Aborigines Mission at the Warburton Range, established in 1935 and the Giles Weather Station established in 1956. The mission now has a population of some 300 natives. Most of the mountain area is an Aboriginal Reserve but it seems that in recent years the native population has become concentrated at the mission so that there are no longer any people living and hunting in the wild further out. The population of Europeans is a handful at either settlement. There are no sheep or cattle on the country anywhere and kangaroos and emus appear to be very sparse. Fresh camel tracks were frequently seen by us, but no actual animals. No trace of rabbits was observed.

Meteorological observations have been recorded at the mission since 1940 and at Giles since 1956. These will be discussed later. The annual average rainfall in both cases has been 8½ inches.

Vegetation

The principal vegetation types are (1) scrub heath on sand dunes, (2) tree and shrub steppe on sand plains, (3) mulga scrub on red loam soils and on rock and (4) so-called "mulga

* King's Park and Botanic Garden, Perth, Western Australia.

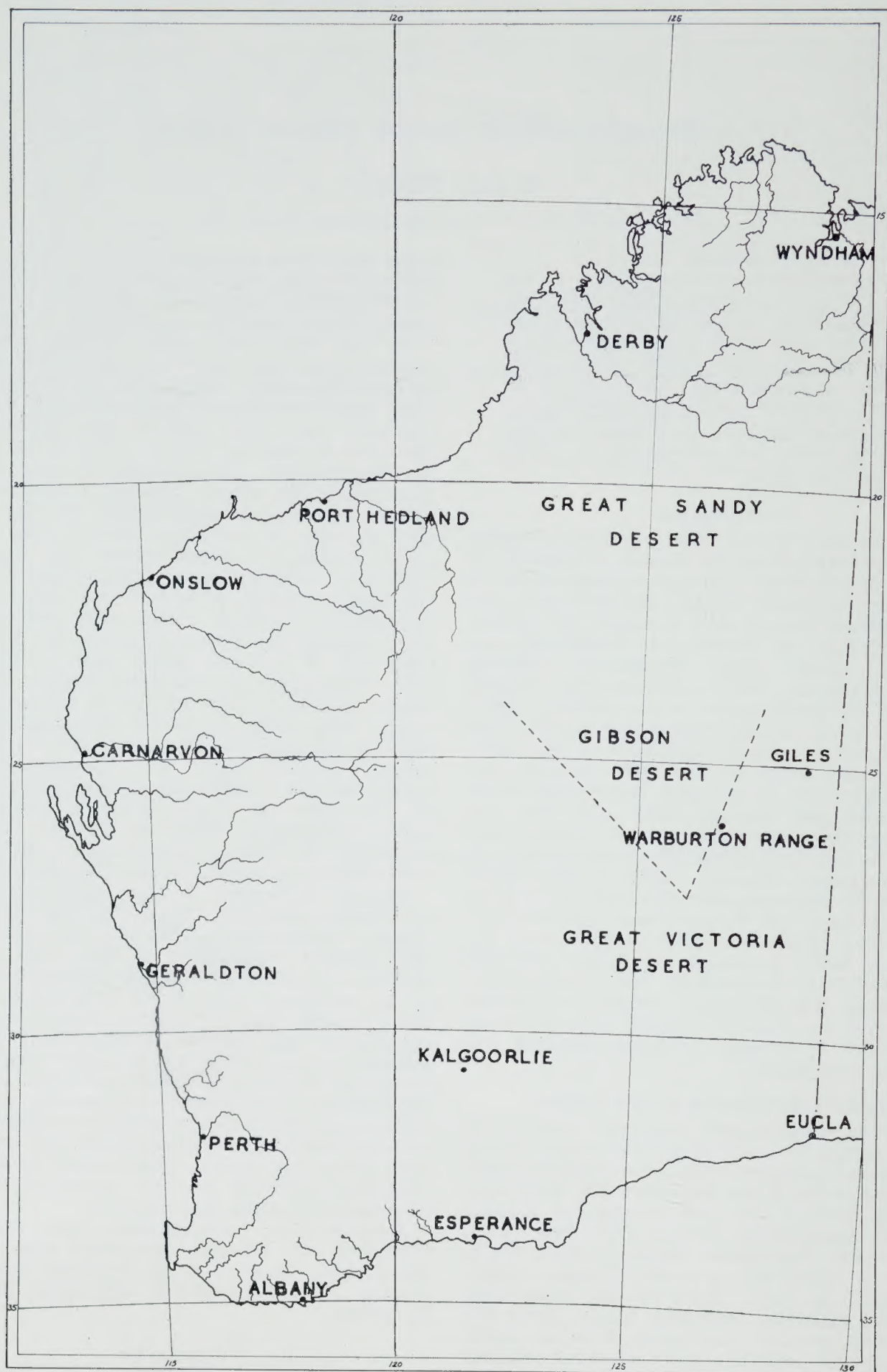


Figure 1.—Map of the area studied, showing localities mentioned in the text.

parkland" on laterite plains. Minor communities which are outside the scope of the present paper include mallee which in this region is confined to kunkar soils in depressions and near salt lakes, only accounting for small areas; a range of salt-tolerant communities in lake beds, and low wattle scrub on the mountain ranges.

1. Sand dunes

The vegetation of sand dunes is very consistent throughout the region and differs markedly from that of dunes in the Great Sandy Desert further north which is a spinifex or steppe formation with *Plectrachne schinzii* dominant, and scattered shrubs and trees. Here in the south both *Plectrachne* and *Triodia* do occur, but sparingly, dominance being assumed by the low ericoid shrub *Thryptomene maisonneuvii* which frequently forms an almost continuous cover especially on the lower flanks of the dunes. It is rather more sparse on their crests. Taller species of shrubs up to 6 ft. tall occur widely spaced, and are at their most frequent along the crests and upper flanks of the dunes. In this class *Grevillea stenobotrya* and *Acacia salicina* are most consistent components. Others include *Grevillea pterosperma*, *Gyrostemon ramulosus*, various species of *Eremophila*, an *Anthotroche* and *Crotalaria cunninghamii*. Other low shrubs include *Micromyrtus flaviflora*. Rather rarely there appear along the crests of the dunes odd trees of the desert bloodwood (*Eucalyptus* sp. aff. *cliftoniana*), a species which is here at the limit of its range, being much more common in the Great Sandy Desert. It was not observed at all south of the 27th Parallel.

With only these few trees and a few scattered plants of spinifex this is essentially a shrub community which in both physiognomy and floristic composition is related to the scrub heaths of the Southwestern Province which in the same way feature a low, more or less continuous stratum of ericoid shrubs belonging mainly to the Myrtaceae with an open upper stratum mainly of Proteaceae with some *Acacia*.

Where sandhills are close together, the dune scrub is continuous. Where they are widely spaced other vegetation occurs between them and is usually either mulga or tree/shrub steppe according to soil.

2. Sand plains

It is perhaps curious that the vegetation of flat sandy areas is entirely different from that of sand dunes. Invariably in this region sand plains carry hummock grassland, or steppe in the sense of Gardner (1942) and Beard (1966). *Triodia basedowii* is the almost universal constituent, together with a tree or shrub component which varies locally. The Great Victoria Desert is characterised by the mallee *Eucalyptus pyriformis* and the tree *Eucalyptus gongylocarpa* which frequently associate but perhaps as frequently occupy separate areas. In the southern part of the Great Victoria Desert open, park-like stands of *E. gongylocarpa* with a spinifex floor are common and form an attractive landscape but devoid of any other conspicuous plant species. Shrub steppe of *E. pyriformis* on

the other hand generally has numerous associated shrubs including *Hakea microneura*, *H. lorea*, *Grevillea juncifolia*, *Acacia salicina*, *A. helmsii*, *Melaleuca* spp. and *Wehlia thryptomenoides*. Within the Great Victoria Desert the two eucalypts tend to invade the sandhills, of which the vegetation becomes more mixed.

In the general area of the Rawlinson Range complex there is a widespread occurrence of tree steppe formed by the desert oak, *Casuarina decaisneana*, over a spinifex floor of *Triodia basedowii*. The *Casuarina* trees grow to 40 ft. tall and form open stands of pleasing appearance. There are no conspicuous associated species.

A minor shrub steppe community found on sand in the Gibson Desert is one of *Grevillea juncifolia*, *G. eriostachya*, *Hakea lorea*, *Acacia linophylla*, *Eremophila leucophylla*, and frequently *Eucalyptus gamophylla* (a mallee) over *Triodia basedowii*.

3. Mulga

The mulga formation is an open community of large shrubs mostly about 10 ft. tall but reaching twice this height or more in favourable situations with adoption of a tree habit (i.e. a definite trunk instead of branching from the base). *Acacia aneura* is the sole species in this layer. In a pure mulga formation on heavy loam flats there may be sparse undershrubs of *Eremophila* spp. and *Ptilotus obovatus* but the soil is normally quite bare except for ephemerals in season—annual grasses and composites. Where the soil becomes more sandy, *Triodia basedowii* comes in and occupies the ground to some extent. On rocky ground such as along the tops of breakaways a stunted mulga is found.

Through this whole region mulga is typically to be found along lines of breakaways, on top and at the foot, and forms patches between dunes in sandhill areas. It will also occupy plains of red loam soil in sand-free areas, particularly in the vicinity of the hill ranges in the Warburton-Giles sector, and is an important component of the mosaic on laterite plains as will be shown in the next paragraph.

4. "Mulga parkland"

The extensive rolling laterite plains of the Gibson Desert are vegetated with a mosaic of intergrading communities of mulga, shrub steppe and grass steppe which as a whole may be conveniently regarded as an attenuated mulga formation and termed the mulga parkland. Patches of typical dense mulga scrub occupy substantial portions of the laterite plains, generally in dips, depressions or drainage lines but at times with no obvious topographic control. Such patches, which have a bare floor, grade outwards into mulga with a spinifex floor and this in turn opens out with the mulga becoming sparser, and associated with other species. At this stage there is a recognisable shrub steppe association, which may be called the *Hakea-Acacia* shrub steppe. Characteristic species are *Hakea lorea*, *Acacia pruinocarpa* and *Acacia aneura* which are all very consistent, and, rather more sporadically, the mallee *Eucalyptus kingsmillii*, *Acacia grasbyi* and *Eremophila leucophylla*. In the poorest and stoniest parts the



Figure 2.—Effect of drought on sandhill vegetation. Gunbarrel Highway west of the Rawlinson Range.

shrub steppe opens out still further tending almost to a pure grass steppe of spinifex hummocks alone. On such sites the visible ground is surfaced with a desert pavement or *hamada* of rounded pieces or ironstone up to 2 inches in diameter (Fig. 8). Underlying "soil" (if that term is applicable) consists of about 6 inches of loose friable ironstone gravel overlying a massive indurated layer. In the direction of dense stands of mulga the top soil contains a higher proportion of loam with the ironstone component contracting to small nodules.

General note

It will be observed that this desert area is vegetated with plant formations which extend elsewhere and are already known in other parts of Australia. The inaccessibility and resulting ignorance of this region hitherto have led to a number of misconceptions becoming current, as is evident for example from Hall et al (1964), who state, apropos of a study of the Koonamore Vegetation Reserve in South Australia, situated in a mulga belt: "The 10 most common tree and shrub species found on Koonamore Vegetation Reserve are widely distributed across Australia, especially in an East-west direction . . . the Nullabor Plain and the Great Victoria, Gibson and Simpson Deserts are too arid for the survival of these species. The odd plant found within these areas has always been noted near

a water source." This observation shows both the inadvisability of relying on herbarium records for distribution and the need for botanical collectors to record more ecological data. Two of the commonest species at Koonamore, *Acacia aneura* and *Casuarina cristata* occur throughout the Nullabor Plain, Great Victoria and Gibson Deserts wherever the particular soil type with which these species are associated occurs. In terms of rainfall and vegetation the Great Victoria and Gibson "Deserts" are not more arid than other parts of the interior adjacent to them. Their reputation as deserts appears to derive partly from the abundance of sandhill tracts and partly the want of surface water supplies, and both of these features are directly due to the geological structure of the country as a lowlying sedimentary basin.

Drought effects

Some of the more severe observed effects of drought are illustrated photographically in Figures 2-9. Figure 2 shows a sandhill with 2 desert bloodwoods against the skyline, both of which have died back very substantially and are now making weak epicormic growth. The slopes of the sandhill were clothed with bushes of *Thryptomene maisonneuvii* most of which have died, and with clumps of spinifex which



Figure 3.—Sandhill area severely affected by drought. On Sandy Blight Junction Road near Lake Hopkins.



Figure 4.—Desert oak grove partially killed by drought. Same area as Figure 3.

have fared rather better and come back into full vigour. Regeneration on the dune includes many pioneer subshrubs such as *Dicrastyles*.

Figure 3 is taken from the top of a sandhill in a particularly drought-stricken area near Lake Hopkins. The Walter James Range is visible at upper right, and the flat at lower right carries large desert oaks nearly all of which have died (see also Fig. 4). On the sandhill itself almost every plant died. Shrubs in the foreground are dead or almost so, and in the distance a few dead desert bloodwoods can be seen. Little or no regeneration had taken place here.

Figure 4 was taken only a few yards from Figure 3 and shows the desert oak grove in the flat, most of the trees dead and with their bark dropping off. Some in the rear have survived. Presumably no drought of this severity had occurred within the lifetime of these trees. The spinifex here had survived well though badly damaged, and at the time of the visit there was a good crop of yellow daisies which show up (*Helipterum stipitatum*).

Figure 5 shows a severe case of destruction of mulga, where a whole stand has perished leaving only bare earth with a few sparse clumps of annual grass. Such cases are fortunately rare, the more usual effect being as in Figure 6 where some only of the mulga bushes have died. In Figure 7 there had been copious regeneration of mulga already man-high.

Figure 8 shows the surface of a laterite plain of the Gibson Desert strewn with ironstone fragments. Former large spinifex clumps at lower left and upper right have died and partly rotted away, while small spinifex seedlings can be seen in process of replacing them. There is one just to the right of the centre of the photograph. It is interesting to note accumulation of small buckshot sized ironstone pebbles on the site of the old spinifex clumps, presumably due to sorting by wind.

Figure 9 shows an area of grass steppe in the Gibson desert where spinifex died or largely died back. Most of the spinifex visible is dead but some clumps have made regrowth. Regeneration in this case has been in the form of a lush growth of pioneer subshrubs and forbs, flowering when the photograph was taken. These included *Dicrastyles exsuccosa*, *Burtonia polyzyga*, *Halgania solanacea*, *Goodenia azurea*, *Trachymene glaucifolia* and three species of *Ptilotus*. It is interesting to note that a similar succession is observed in pastoral country in north-western Australia following deliberate burning of the spinifex for purposes of range management. Rapid seedling regeneration of *Triodia* is accompanied by a luxuriant crop of annuals, perennial forbs and subshrubs such as many species of *Ptilotus*, *Clianthus formosus*, *Goodenia stapfiana*, *Trachymene glaucifolia* and *Keraudrenia integrifolia*. The latter grow and flower luxuriantly for several



Figure 5.—Dead mulga. Gunbarrel Highway near the Todd Range.



Figure 6.—Mulga partly affected by drought. Gunbarrel Highway west of the Barker Range.

seasons, given adequate rains, but gradually recede as the spinifex becomes more fully established, eventually becoming rare and inconspicuous in a matured spinifex community.

Naturally the question arose as to whether the observed effects of death and regeneration resulted from fire and not drought, but this was easily decided by inspection of remaining dead material. Spinifex which is burned is completely consumed whereas remains of dead clumps were everywhere visible, some re-sprouting. Little if any of the dead woody plants in affected areas that were examined exhibited any signs of charring. This is not to say that fire does not occur in this type of country. No sign of any recent burn was seen anywhere during the whole trip of our party and the mission superintendent stated that bushfires did not occur in that country. Nonetheless signs of charring on old dead trees, stumps and logs could very frequently be seen. In the records of all the 19th century explorers, e.g. Lindsay 1893, it will be found that smoke from native fires was seen every day, and not of camp fires but of vegetation lit up for signals or hunting purposes. On approaching Queen Victoria Spring Lindsay recorded that most of the country had been burnt off and in one area an extremely severe fire had occurred about 2 years before.

Since the aborigines have become concentrated at the mission it appears that firing of the country has abated, so that in time some interesting vegetational changes may result.

The photographs reproduced were naturally taken of the most obvious and severe cases of drought effects which were patchy in their incidence. The photographs are therefore not typical of the region as a whole, the general average being much less severely affected, with many patches undamaged. This is to be expected; rain, especially when shed from thunderstorms, falls irregularly and soils vary in their moisture-holding capacity. Almost everywhere, however, at least some degree of damage was noticeable in death and dieback of plants.

Climatic data

Meteorological data have been recorded at the Warburton Range Mission since December 1940 and at the Giles Weather Station since September 1956. The figures were kindly made available to the writer by the Commonwealth Bureau of Meteorology. Records are continuously available for Giles, but four months' records—September to December 1940—are missing at the Warburton Range. Only the Warburton figures are used here for the climate

TABLE 1

Monthly Rainfall records at Warburton Range mission

Rainfall in hundredths of an inch

	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Total
1941	0	182	330	92	43	54	31	7	2	61	112	118	1032
1942	697	272	710	41	143	242	12	20	1	12	328	241	2719
1943	6	82	112	333	50	0	0	0	6	27	28	11	655
1944	7	0	4	303	4	10	14	115	17	17	59	140	690
1945	63	18	389	0	28	99	114	42	56	39	20	13	881
1946	12	480	125	4	19	48	6	0	no records				
1947	81	42	76	3	0	109	38	185	34	188	180	375	1311
1948	6	21	6	435	12	0	16	0	0	3	47	67	613
1949	1	202	15	0	276	10	1	3	7	0	106	45	666
1950	49	274	0	0	357	82	23	1	7	169	106	61	1129
1951	104	69	9	16	0	140	1	0	95	0	95	10	539
1952	189	7	34	24	251	12	54	49	16	165	142	35	978
1953	100	15	0	86	98	8	6	58	0	95	5	157	628
1954	22	0	0	274	112	25	10	4	0	102	0	63	612
1955	36	14	140	137	27	388	211	228	0	0	146	0	1327
1956	3	0	12	3	134	124	190	25	0	3	77	11	582
1957	38	144	13	0	16	98	36	14	12	17	0	239	627
1958	22	0	266	0	63	60	114	284	8	1	22	152	992
1959	37	27	0	73	0	39	99	0	3	0	4	107	389
1960	190	587	1	120	93	23	6	7	18	2	0	315	1362
1961	4	35	0	84	0	2	0	0	8	4	0	0	137
1962	39	52	22	57	64	0	68	13	0	150	8	19	492
1963	94	29	41	0	66	86	3	2	0	14	10	86	431
1964	32	0	0	199	73	17	0	389	60	0	105	193	1050
1965	0	0	80	0	28	20	55	0	0	7	144	60	394
1966	31	300	7	200	66	144	0	27	0	48	103	24	950
25 year average	74	95	91	99	80	72	44	59	14	45	78	102	853
No. of months receiving 0	2	6	6	7	4	3	4	6	9	5	5	2	59
No. of months receiving <.10 in.	8	7	11	9	5	7	10	12	17	11	9	3	110
Highest recorded	697	587	710	435	357	388	211	389	95	188	328	375	2719
No. of months receiving > 1.00 in.	5	8	7	8	6	6	5	5	0	4	9	10	73

analysis as they cover a longer period. Since 1956 the Giles figures have been closely comparable each month.

Considering first the monthly and yearly rainfall totals, given for the Warburton Range in Table 1, it will be seen that over the 25 years of records the annual rainfall has varied between 27.19 and 1.37 inches, averaging 8.53 inches. In an arid region of this kind average figures are not of great value, since it is critical extremes which are significant for vegetation. However, some discussion of both is desirable. Average monthly distribution, given at the foot of Table 1 as the "25-year average", appears to show a bias towards summer and early winter rainfall, with a relatively dry spring, September being a generally dry month. On the other hand the next line at the foot of the table shows that nil rainfall may be recorded in any month of the year with no conspicuous monthly bias except towards September. The next line again, for "negligible rains" of under 0.10 inches, shows rather more seasonal variation with a high figure for March—perhaps an intermission between summer and winter rains—and a high group in spring. Below this, an extraction of the highest monthly total on record shows little seasonal variation except a September-October drop. The last line gives the number of months in which appreciable rainfall of 1.00 inch or over has been recorded. The spring drop is again apparent. Such rainfall was received in 73 months out of the 300 in the 25-year period of records, or approximately 1 month in 4.

It is apparent from the monthly summaries that rainfall here is extremely erratic and unreliable with little seasonal pattern.

According to residents at the Warburton Range Mission, the 3 most recent seasons 1966, 1965 and 1964 had all been good years locally, whereas at least 3 years prior to that had been drought years. This is consistent both with field observation of a recent regeneration period of several years' duration, and with the monthly rainfall records. During the initial 18 years of records up to and including 1958 the lowest annual rainfall total was 5.39 inches. 1959 was a dry year with only 3.89 inches but was followed by a wet year with 13.62 inches. 1960 was the driest year on record with only 1.37 inches and was followed by 2 more dry years with totals of 4.92 and 4.31 inches in which rain was only light. The drought was not broken until April 1964.

More detailed evidence is obtainable from the daily rainfall records, computed in the form of "rain events" rather than the daily rainfall totals. Daily rainfall at 9 a.m. may be misleading as to effectiveness of precipitation. If rain is in progress at the time of measurement, a single fall may be split between two days. Conversely it will be readily understood that an isolated fall of .50 inch is not likely to be very effective in this arid region, whereas .50 inch received daily for five days is very likely to be effective and therefore is best recorded as a single "event" of 2.50 inches. A rain event is defined as precipitation received on two or more consecutive days.

If the 20 years of records from January 1941 to December 1960, complete except for 4 months of 1946, are examined for evidence of an average pattern prior to the drought, 445 rain events of any magnitude ($> .01$ inch) were recorded, averaging 23 per year, the interval between them varying from 1 to 98 days, with a mean of 14.5 days. Most of these events were however weak and doubtfully effective. The question of rainfall effectiveness in the interior has been discussed by Slatyer (1962) for the Alice Springs area and Arnold (1963) for the Meekatharra-Wiluna area in Western Australia. The latter found that the

rainfall sufficient to initiate plant growth varied from as little as 0.24 inch in July to 1.18 inches in December. It seems unnecessary in the present case to make the elaborate calculations embodying evaporation data which were employed by Arnold, especially as evaporation has not been recorded at the Warburton Range meteorological station. Effective rain events have been estimated instead on the basis of notes made by the observer there on growth of grass and wildflowers, and generally a figure of .80 inch is taken as the threshold. Events between .25 inch and this level are listed as minor effective rains with this result:—

	Total No. of events	Mean No. of Events per year	per cent total rainfall
20—year period 1941–1960			
—ineffective rain events $< .25$ inch		14.7	15
—minor effective rains		4.2	21
—major effective rains $> \pm .80$ inch		3.3	64
		22.2	100
Drought period Jan. 1961—April 1964 (40 months)			
—ineffective rain events $< .25$ inch	46	13.8	43
—minor effective rains	14	4.2	47
—major effective rains $> \pm .80$ inch	1	.03	10
	61	18.3	100



Figure 7.—Dense regeneration of mulga after drought, 10 miles north of Warburton Range Mission.



Figure 8.—Surface of laterite plain of the Gibson Desert showing hamada surface and regenerating spinifex seedlings among dead clumps.

It will be readily seen that in a "normal" period the vegetation is maintained by the occasional heavy soaking rains which may be expected about every four months on the average and account for two-thirds of all the precipitation. In practice, between 1941 and 1960 the interval between such falls varied from 3 to 376 days: it 4 times exceeded 300 days and 8 times 200 days. Droughts of up to a year are therefore common and are tolerated by the plant cover. During the severe drought period, the number and frequency of light ineffective rains remained more or less constant, but the heavy soaking rains virtually ceased. The drought began after three intermittent rain events totalling 2.79 inches during the week 14-21 December 1960. A rain event of 1.15 inches occurred over the four days 15-18 October 1962, 22 months later. In the meantime there had been five events between .30 and .40 inch, and three respectively .47, .53 and .57 inch, all dubiously effective. Heavy soaking rain did not recur until 28th April 1964, a further 18 months during which only light rain was received. The drought was broken at this point by a fall of 1.45 inches over 2 days, followed by 2 light falls in May (.28 inch and .45 inch) and 3.86 inches in August of that year. Subsequently the pattern of intermittent heavy rain was resumed to give the "good seasons" reported by the local residents, the

relative rain events being 3.86 inches, 29-31 August 1964 : 1.85 inches, 20-21 December 1964 : 1.44 inches, 28 November 1965 : 3.00 inches, 14 February 1966 : 2.56 inches 25 April to 4 May 1966 : 1.41 inches, 26-29 June 1966. The drought therefore lasted forty months.

Discussion

Since rainfall is notoriously variable it is to be assumed for any arid or semi-arid region that periodic droughts will occur which will adversely affect vegetation. On the other hand it also tends to be generally assumed that the vegetation of arid areas is adapted to this, the plants concerned being capable of survival by prolonged dormancy. For the general run of drought periods this is no doubt true and in this particular case we may have encountered the rare drought of exceptional severity. This view is favoured by the observation that mature desert oaks 40 feet in height died, so that presumably no drought of comparable severity had occurred during their lifetime. Rainfall records have not yet extended over a sufficiently long period to throw any light on this, but it is of interest to quote the observations of D. Lindsay (1893) who in 1891 led the Elder Exploring Expedition in a crossing of the Great Victoria Desert. The explorers Giles and Forrest in their visits to this



Figure 9.—Laterite plain 60 miles west of the Warburton Range Mission with pioneer growth of flowering subshrubs and forbs following death of spinifex.

area in 1875 and 1876 had encountered good seasons with abundant feed and water, but in 1891 on crossing the West Australian border from the east, west of the Blyth Range, Lindsay's party "entered a region so dry as to lead us to the conclusion that no rain had fallen for two or three years . . . even the spinifex was dead . . . and the mulga nearly so." (loc. cit. p. 6).

Some interesting observations are also to be found in the report of the surveyor H. L. Paine who ran a traverse from Laverton to the Warburton Range in 1931 (quoted in *Cartography in Western Australia*, 1966)

"From the Elder Creek eastward to the Barrow Range, northward to the latitude of Spring Granite and southward to the Townsend Range, an area which was examined by myself, had enjoyed a good seasonal rainfall and was carrying a great growth of herbage and wandarie grasses. This seasonal growth is, of course, absolutely dependent on the rainfall and I am of the opinion that this area of country is subject to great irregularity in this respect. (Reference to photographs numbers 7, 8 and 9 show much dead mulga and very little regrowth—practically no scrub feed whatever). Previously this country had been examined by Mr. Frank Hann in 1903, and Mr. H. B. Talbot in 1916, and they both reported as subject to long droughts; and I must agree also."

It now seems necessary to suppose that in these dry regions, regeneration of plants is cyclic and not continuous. Instead of a steady process

of recruitment by seedlings replacing individuals which have died of old age, the sort of process expected in moist forests for example, we must suppose that at certain intervals the community is more or less wiped out, regenerating when the drought is broken. Each community in this case would be what foresters call an even-aged stand. It also follows that there may be no consistency of floristic composition in succeeding cycles. If the climatic conditions for regeneration vary, as they may well do, one species may be favoured against another so that the relative numbers of those in the stand may vary. Any floristic studies made should take this into account. The same argument applies to communities which are regularly burnt, if regeneration is effected by seed rather than coppice. There is no guarantee that the floristic composition of a community has any continuity in time in these cases.

Mortality due to drought in arid regions of Australia, and cyclic regeneration, have of course been observed and reported before in Australian literature, but not quite in these same terms. Melville (1947), Everist (1949, 1960), Parkinson (1960-61) and Hall et al. (1964) have all reported that mulga regenerates copiously in years of abnormally heavy summer rain, so that mulga stands tend to consist of even-aged groups. Parkinson (ibid) also noted that "cycles of re-

generation of many species of trees and shrubs appear to occur for no apparent reason." Catastrophic mortality from drought seems to have been little reported. Pook, Costin and Moore's (1966) interesting paper does not deal with a normally arid area. Everist (1949) recorded that after the drought of 1943-46 large numbers of dead mulga trees were to be seen in South-western Queensland. He investigated this in detail in 1948 and found that the drought tended to have had a thinning effect, reducing more heavily stocked stands to about 250 trees per acre : stands already at or below this figure being little affected. This is perhaps in essence what the present writer also observed in mulga, in the discussion in this paper on Figures 5 and 6 (see page 44).

In the literature there does not seem to be any suggestion of a cycle embodying both drought mortality and subsequent regeneration, only of intermittent regeneration in heavy rainfall years. This may indicate that widespread catastrophic drought mortality is a rarity, but it may also be remarked that regeneration in wet years is not likely to survive in competition with fully stocked stands (Zimmer 1944) and probably depends on some previous depletion of the plant cover for its establishment.

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5.—Revision of the *Egernia whitei* species-group (Lacertilia, Scincidae)

by G. M. Storr*

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Abstract

The *Egernia whitei* species-group is confined to Tasmania and the southern two-thirds of Australia and consists of eight species: *margaretae* nov., *pulchra* Werner, *whitei* Lacépède, *multiscutata* Mitchell & Behrndt, *slateri* nov., *inornata* Rosén, *striata* Sternfeld and *kintorei* Stirling & Zietz. The first three species comprise the *E. whitei* superspecies. The last three species are monotypic; the others are divisible into two or three subspecies, including *margaretae personata* nov., *pulchra longicauda* Ford, *whitei modesta* nov., *whitei tenebrosa* Condon, *multiscutata bos* Storr and *slateri virgata* nov.

Introduction

One might question the validity of a species-group that embraces such diverse forms as *Egernia kintorei* and *E. pulchra longicauda*. Yet these taxa are connected by a chain whose adjacent links are so similar as to make it hard to devise keys and diagnoses for their separation. It is this continuity in adaptation and morphology that defines the species-group rather than any characters that all its components might share.

It is also due to this continuity that it has proved one of the most perplexing groups of Australian lizards. Earlier workers were hampered by paucity of material and lack of ecological data, two deficiencies that have been made abundantly good by recent field-work in the interior, notably by K. R. Slater and his colleagues at Alice Springs.

Nevertheless, even with 1,150 specimens before me, I have often failed to find really good diagnostic characters. As there is usually much overlap in scutation, proportions and meristics between related species, one must largely rely on differences in colour and pattern. This is unfortunate, for in several taxa coloration is subject to much individual or ontogenetic variation. Consequently it is feared that students with few and poorly preserved specimens will have trouble in identifying them. A brief preview of the species may be helpful.

Six of the eight species can be allotted to one or other of two sections:

(1) The *Egernia whitei* superspecies (comprising the semispecies *whitei*, *pulchra* and *margaretae*). These are dark or drab lizards with relatively long flat heads, depressed bodies and slender appendages. They live among rocks or plant debris in the more humid parts of southeastern and southwestern Australia, with outlying populations in the mountains of northern South Australia and the south of the Northern Territory. As all these lizards are allopatric, they can at last resort be identified on geography.

(2) *E. inornata*, *striata* and *kintorei*. These are reddish or yellowish lizards with relatively short deep heads, deep bodies and short thick appendages. They live in complex burrow-systems in arid and semiarid regions. Because they are broadly sympatric they can only be identified on morphology. *E. inornata* should never be hard to distinguish from the other two. However the separation of *striata* and *kintorei* may require in some cases the simultaneous consideration of several characters.

The remaining species, *multiscutata* and *slateri*, variously combine the characters of the two sections. *E. multiscutata* could only be confused with members of the *whitei* superspecies with which it is partly sympatric. *E. slateri* could only be confused with *inornata* or *striata*, both of which occur throughout its restricted range.

In the following descriptions quantitative characters are expressed as ranges. Means are not given here, for they are of little value in diagnosis; they are more useful in providing a picture of intragroup trends and so are brought together in one place (Table 1). Relative length of appendages must be used with some caution in diagnosis, for it changes with growth. The limbs are relatively much longer in juveniles than adults. Therefore if the snout-vent length indicates that a specimen is adult, its relative length of foreleg and hindleg should be close to the lower limits given for that taxon. Relative length of tail, however, is usually greatest in young adults.

Among the characters studied are two that require explanation: "upper palpebrals" refer to the series of enlarged whitish scales along the free edge of the upper eyelids; "calli" are subdigital thickenings that are too obtuse to be called keels. Snout-vent length is often abbreviated to SVL.

During this revision I have studied all the material in the Western Australian Museum (WAM) and have borrowed most of the specimens in the collections of the Animal Industry Branch, Alice Springs (NTM), South Australian Museum (SAM), National Museum of Victoria (NM), Australian Museum, Sydney (AM), Queensland Museum (QM) and Queen Victoria Museum, Launceston (QVM). For these loans I am grateful respectively to Messrs K. R. Slater, F. J. Mitchell, J. McNally, H. G. Cogger, J. T. Wood and W. F. Ellis. I am also grateful to Dr Eric Pianka for the loan of specimens he collected in the southern interior of Western Australia, and to Lt-Cdr A. Y. Norris for the opportunity to examine the collection made by the British Joint Services Expedition (JSE) to Central Australia in early 1967. Finally I am indebted to Mr. K. R. Slater for data on the ecology and pupil-shape of the Northern Territory species.

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TABLE 1

Number of specimens (number with original tail in parentheses), mean snout-vent length (mm), mean length of appendages (as per cent SVL) and mean number of midbody scale-rows, lamellae under fourth toe, supraciliaries, upper palpebrals, upper labials and ear lobules.

	Number	SVL	Tail	Foreleg	Hindleg	Scale-rows	Lamellae	Supraciliaries	Palpebrals	Labials	Lobules
<i>m. margaretae</i>	17 (3)	95	181	25.7	35.3	35.6	22.4	8.1	11.2	8.0	3.6
<i>m. personata</i>	12 (8)	89	169	29.3	40.8	40.9	23.2	7.9	12.8	8.4	2.8
<i>p. pulchra</i>	26 (12)	89	168	28.0	38.6	36.4	25.2	7.5	11.5	7.2	3.1
<i>p. longicauda</i>	16 (6)	91	196	28.6	39.2	35.4	26.1	8.1	11.6	7.9	3.2
<i>w. whitei</i>	16 (9)	85	168	27.9	38.7	37.2	24.6	7.4	11.6	7.4	3.2
<i>w. modesta</i>	20 (10)	95	165	25.8	35.9	37.0	23.1	7.7	12.1	8.0	3.7
<i>w. tenebrosa</i>	262 (116)	71	150	27.0	37.8	35.2	21.3	6.9	10.5	7.4	3.3
<i>m. multiscutata</i>	8 (2)	67	160	32.6	45.7	42.7	24.0	7.1	9.9	8.0	3.7
<i>m. bos</i>	97 (40)	72	149	30.5	40.9	41.7	24.0	7.8	10.7	7.8	4.0
<i>inornata</i>	246 (83)	65	125	28.5	38.2	37.4	23.5	7.5	10.7	7.0	3.8
<i>s. slateri</i>	89 (30)	75	130	29.3	38.8	39.7	22.1	7.4	11.1	7.1	4.3
<i>striata</i>	288 (136)	86	128	28.0	36.2	41.1	21.0	8.4	12.5	7.1	4.8
<i>kintorei</i>	46 (20)	160	111	26.7	32.7	47.6	20.2	8.4	14.6	8.1	4.9

Key to species and subspecies

- 1a. Dorsal ground coloration generally dark and dull (olive, grey, brown, fawn or chestnut) usually patterned with black longitudinal stripes, lines or rows of blotches; most ventral surfaces pale grey (at least in alcohol); head and body depressed or deep; tail 1.1-2.2 times as long as head plus body 2
- 1b. Dorsal ground coloration generally pale and bright (yellowish, fawn or reddish), either completely lacking black markings or dotted with black; head and body deep; tail 0.9-1.5 times as long as head plus body 10
- 2a. Dorsal scales smooth 3
- 2b. Dorsal scales keeled 5
- 3a. Conspicuous black callus along free edge of subdigital lamellae; scales of soles and palms each with a prominent black tubercle 4
- 3b. Subdigital lamellae smooth or with one or two series of pale or dark brown longitudinal calli or keels; soles and palms smooth or with small white or dark tubercles 6
- 4a. Dorsally dark olive grey or brown (sometimes suffused with dull chestnut) with or without black spots which tend to align longitudinally; snout no more depressed than rest of head, edges straight in plan; midbody scale-rows 38 or fewer *margaretae*
margaretae
- 4b. Dorsally pale olive grey or brown, with or without black longitudinal lines (remnants of laterodorsal stripes); snout strongly depressed, edges concave in plan; midbody scale-rows 38 or more *margaretae*
personata
- 5a. Nasals in contact or narrowly separated; upper labials usually 8; tail 1.8-2.2 times SVL; venter suffused with orange in life *pulchra*
longicauda
- 5b. Nasals widely or narrowly separated; upper labials usually 7; tail 1.6-1.8 times SVL *pulchra*
pulchra
- 6a. Interparietal much narrower than frontal in adults (slightly narrower or as wide in juveniles); head and body slightly to moderately depressed; midbody scale-rows 30-42 7
- 6b. Interparietal slightly narrower or wider than frontal in adults (much wider in juveniles); head and body deep or slightly depressed; midbody scale-rows 38-46 9
- 7a. Conspicuous white streak along upper half of upper labials, posteriorly bordered below by black streak; black laterodorsal stripe ragged-edged when present; tail heavily stippled with black; scales of soles and palms with or without small dark tubercle *whitei*
whitei
- 7b. Pale labial streak absent or obscure, posteriorly bordered or not by brown streak; usually only base of tail patterned; palms or soles with or without small white tubercles 8
- 8a. Adults unpatterned and usually more than 95 mm in SVL; nasals narrowly separated; proximal subdigital lamellae usually with high calli *whitei*
modesta
- 8b. Adults usually less than 95 mm in SVL; adults (like juveniles) may lack pattern on back and sides, but usually have sharp-edged black laterodorsal stripe (enclosing a series of pale spots) and ocellate flanks; nasals usually widely or moderately separated; proximal subdigital lamellae smooth or with low calli *whitei*
tenebrosa
- 9a. Broad black laterodorsal stripe enclosing two (sometimes one) series of pale spots or short lines; subdigital lamellae usually bicarinate *multiscutata*
subsp.
- 9b. No broad black laterodorsal stripe enclosing pale spots; subdigital lamellae compressed, with an apical series of calli 11
- 10a. Sides (especially dorsolaterally) and often back spotted finely with black; orbits black; pupil circular or a little narrower than high; SVL less than 85 mm *inornata*
- 10b. Black pigment completely absent; pupil narrowly or broadly elliptical; SVL of adults more than 85 mm 12
- 11a. Dorsal pattern consisting of several black (or dark brown) broken longitudinal lines *slateri*
slateri
- 11b. Dorsal pattern consisting of a black vertebral stripe, widely separated from a broken laterodorsal stripe *slateri*
virgata
- 12a. SVL less than 120 mm; pupil much narrower than high; back reddish brown, longitudinally striped with dark reddish brown; ground coloration gradually becoming greyish brown on sides; upper labials usually 7; presuboculars usually 2; midbody scale-rows usually fewer than 46 *striata*
- 12b. SVL of adults more than 150 mm; pupil slightly narrower than high; back pale reddish brown with or without slightly darker longitudinal stripes; lateral coloration grey, sharply demarcated from dorsal; upper labials seldom fewer than 8; presuboculars seldom fewer than 3; midbody scale-rows seldom fewer than 46 *kintorei*

Egernia margaretae margaretae subsp. nov.

Holotype.—R 29129 in Western Australian Museum, formerly NTM 2351, an adult male collected by K. R. Slater and D. A. Lindner on 25 November 1964 at Palm Valley, Northern Territory, in 24°03'S, 132°42'E.

Diagnosis.—A large, dark, long-tailed, short-limbed member of the *E. whitei* superspecies, with head and body strongly depressed, colour pattern obscure or absent, and palms and soles tuberculate.

Distribution.—Central Australian highlands: James and George Gill Ranges of southern Northern Territory, and Musgrave and Mann Ranges of far northwestern South Australia.

Description.—Ear aperture narrow to moderately wide; lobules 3-5, usually obtuse, sometimes rectangular, rarely acute. Snout-vent length (mm): 53-107. Length of appendages (% SVL): foreleg 22-28, hindleg 31-38, tail 172-189.

Nasals moderately to widely separated. Prefrontals usually forming median suture, sometimes just touching or very narrowly separated. Frontal slightly to greatly wider than interparietal. Supraciliaries 8 (rarely 7 or 9). Upper palpebrals 10-12. Upper labials 8 (rarely 7 or 9). Midbody scales smooth, 34-38 rows. Lamellae under fourth toe 20-25, entire or proximally divided, each with a strong dark callus (becoming weaker distally and tubercular proximally). A dark tubercle in centre of each scale of palm and sole.

Dorsally olive brown, paler on tail and sometimes tending to reddish-brown on fore-back. Black spots on back and tail, irregularly distributed or tending to align longitudinally. Sides greyish with black spots tending to form oblique rows directed up and back. Small black spots scattered on top and side of head. Sutures of chin-shields irregularly margined with black. Dark brownish grey spots or short wavy longitudinal lines on throat. In 30% of specimens black markings completely lacking.

Geographic variation.—The two specimens from South Australia have not been used in the above description. Their snout-vent length is 99 and 62 mm. They differ from northern specimens in the very narrow separation of nasals, wider interparietal (as wide as frontal in smaller specimen), fewer supraciliaries (6), more palpebrals (11 and 13), and fewer rows of midbody scales (32 and 36). The smaller has relatively long limbs (31 and 42% of SVL) and is patternless. The larger specimen's pattern merely consists of inconspicuous black spots suggesting the outline of a laterodorsal stripe. This population is separated from the Northern Territory populations by the arid Amadeus lowlands.

Remarks.—Named after Margaret Anne, wife of K. R. Slater, in appreciation of her hospitality. Mr. Slater kindly donated the holotype to the Western Australian Museum.

Paratypes.—Northern Territory: Palm Valley (NTM 2815-8), George Gill Range (NTM 1881-3, 2284-5, 2665-9, 2765-6, 2768-70). South Australia: Piltadi Rockhole (AM 17271), Erliwunyawunya Rockhole (AM 17456).

Egernia margaretae personata subsp. nov.

Holotype.—R 3748 in South Australian Museum, an adult collected by F. J. Mitchell on 26 October 1955 in Wilpena Gorge, South Australia.

Diagnosis.—A pale member of the *E. whitei* superspecies with very little pattern, narrow snout, long appendages, and strongly callose subdigital lamellae. Distinguished from *E. m. margaretae* by paler coloration and longer limbs.

Distribution.—Central and northern Flinders Range, South Australia.

Description.—Body moderately depressed. Snout strongly depressed and concave in plan. Ear aperture usually wide; lobules 2-4, usually obtuse and decreasing in size downwards. Snout-vent length (mm): 57-107. Length of appendages (% SVL): foreleg 27-32, hindleg 37-44, tail 157-177.

Nasals widely separated. Prefrontals forming a long median suture. Frontal much wider than interparietal. Supraciliaries 7-9. Upper palpebrals 11-14. Upper labials 8 or 9. Midbody scales smooth, striate, 38-43 rows. Lamellae beneath fourth toe 21-26, basally divided (rarely entire), each with a broad, high, dark callus (proximally merging with the black tubercles of soles).

Dorsal ground colour greyish or olive brown. Colour pattern greatly reduced; at most only edges remain of black laterodorsal stripe. Pale dorsolateral stripe usually discernible. Flanks obscurely flecked with whitish. Facial markings usually reduced to black orbital mask. Under surface greyish.

Paratypes.—South Australia: North Tusk, Gammon Range (SAM 8724-6), Balcanoona Creek (SAM 3934), Mern Merna (SAM 2645), Wilpena Pound (AM 16628-9), Wilpena Gorge (SAM 8503, 8717-8), 8 mi. SE of Warcowie (SAM 2573).

Egernia pulchra pulchra

Egernia pulchra Werner 1910, in Michaelsen & Hartmeyer's Fauna Südwest-Australiens 2: 470. Torbay, Western Australia.

Diagnosis.—The species *pulchra* is generally similar to *E. whitei* but differs from it and all other species of the group in having keeled dorsals.

Distribution.—The humid southwest corner of Western Australia from Nanga Brook south and east to Cheyne Beach; also in Stirling Range and on Eclipse Island.

Description.—Head and body moderately depressed. Ear aperture moderately wide or narrow; lobules 2-4 (mostly 3), acute or obtuse (sometimes squarish), sharply decreasing in size downwards. Snout-vent length (mm): 47-107. Length of appendages (% SVL): foreleg 25-32; hindleg 33-43; tail 159-181.

Nasals widely or narrowly separated. Prefrontals usually forming a long median suture (sometimes only moderately long, rarely short). Frontal much wider than interparietal in adults, a little wider in juveniles. Supraciliaries 6-8 (mostly 8). Upper palpebrals 10-13. Upper labials 7 or 8 (mostly 7). Midbody scales dorsally and laterally with 2-4 keels (moderately strong

in adults, very weak in juveniles); 34-39 rows. Lamellae under fourth toe 22-30, proximally divided.

Dorsal ground coloration fawn, becoming olive grey on head. A black laterodorsal stripe from nape to base of tail, enclosing a series of pale spots (grey or fawn) and bordered below by a pale grey dorsolateral stripe. Top of head and tail stippled with black. Orbit black, contrasting with creamy white edge of eyelids. Obscure black streak from orbit to temples. Sutures between upper labials margined with black. Sides of body grey, densely stippled with black and sometimes flecked with white. Under surface pale bluish grey.

Geographic variation.—Northern adults (4 from Darling Range and 4 from Stirling Range) have a longer hindleg (38-41, mean 39.9% of SVL) than 10 adults from the south coast (33-38, mean 37.5). In other respects these two widely separated northern populations diverge from the south-coast series in opposite directions, e.g. midbody scale rows and supraciliaries more numerous in the Darling Range, but less numerous in the Stirling Range, than on the south coast. The Darling Range population of *pulchra*, though nearest geographically to *longicauda*, goes hardly any of the way to bridging the morphological gap between the two subspecies.

Remarks.—Although *E. p. pulchra* lacks the conspicuous white labial streak and black facial streaks of *E. w. whitei*, it otherwise resembles it in coloration. This similarity is especially marked in less common variants, e.g. specimens with the black laterodorsal stripe broad and ragged-edged, or those described by Ford (1965) from the Stirling Range which have the back an unpatterned reddish-brown.

Material.—*Western Australia (South-West Division)*: Nanga Brook (WAM 2563), Mt. William (WAM 16784-6), Denmark (WAM 266-8), 24954-8), Chorkerup (WAM 4517), Eclipse Island (WAM 6799, 6800), Two People Bay (WAM 16787-8), Cheyne Beach (WAM 16789-93), Bluff Knoll (WAM 21804, 22862), Mt. Toolbrunup (WAM 21801-2).

Egernia pulchra longicauda

Egernia pulchra longicauda Ford 1963, W. Aust. Nat. 9: 26. Favourite Island, Jurien Bay, Western Australia (J. R. Ford).

Diagnosis.—Differs from *E. p. pulchra* in having tail extremely long, nasals in contact or narrowly separated, and venter suffused with orange.

Distribution.—Islands of Jurien Bay, lower west coast of Western Australia.

Description.—Tail longest in genus. Ear aperture wide; lobules 3 or 4, large, usually obtuse, sometimes acute, usually decreasing in size downwards, suffused in life with orange. Snout-vent length (mm) : 54-104. Length of appendages (% SVL) : foreleg 26-31, hindleg 36-42, tail 180-218.

Nasals usually forming short median suture, occasionally narrowly separated or just touching. Prefrontals forming long median suture. Frontal much wider than interparietal. Supraciliaries 7-9 (mostly 8). Upper palpebrals 10-13. Upper

labials 7-9 (mostly 8). Midbody scales dorsally and laterally with 2-4 keels; 33-38 rows. Lamellae under fourth toe 23-28 proximally divided.

Geographic variation.—All these skinks are fairly similar except for the two from Escape Island, which Ford collected 3-18 months later than the type series. The Escape Island specimens alone retain an orange suffusion over belly, labials and ear lobules. They have 9 upper labials (compared to 7 or 8 in type series) and 10 upper palpebrals (against 11-13). Their limbs are relatively a little shorter than in the skinks from other islands (neither has the tail intact). Both have the nasals separated, compared to only 2 out of 14 from elsewhere.

Remarks.—For ecological relationship of *longicauda* to the Jurien Bay populations of *E. bos* and *E. kingi*, see Ford (1963a, 1965); and for photograph of *longicauda*, Ford (1965).

Material.—*Western Australia (South-West Division)*: Favourite Island (WAM 16769-72, 16781-3), Boullanger Island (WAM 16774-9), Whitlock Island (WAM 16780), Escape Island (WAM 17883-4).

Egernia whitei whitei

Scincus whitii Lacépède 1804, Ann. Mus. Paris 4: 192. New Holland.

Lygosoma moniligera Duméril & Bibron 1839, *Erpétologie générale* 5: 736. New Holland (Péron & Lesueur, Quoy & Gaimard).

Diagnosis.—The species *whitei* is generally similar to *E. pulchra* and *E. multiscutata* but differs from the first in having smooth dorsals and from the second in never having more than one series of pale spots enclosed by black laterodorsal stripe and by its smooth subdigital lamellae. The subspecies *whitei* is large and dark and differs from all others by raggedness of dorsal pattern (when present), black stippling throughout tail and prominent white subocular streak.

Distribution.—Coastal plains and hills of eastern New South Wales from Grafton south to a little beyond Sydney.

Description.—Head and body moderately depressed. Ear aperture wide; lobules 2-4 (mostly 3, seldom 2), obtuse or acute, decreasing in size downwards. Snout-vent length (mm) : 51-113. Length of appendages (% SVL) : foreleg 24-35, 33-46, tail 159-176.

Nasals usually widely, sometimes narrowly, separated. Prefrontals forming a moderate to long median suture. Frontal usually much wider, sometimes only a little wider, than interparietal. Supraciliaries 7-9 (mostly 7, seldom 9). Upper palpebrals 10-14. Upper labials 7 or 8 (seldom 6). Midbody scales smooth, 34-40 rows. Lamellae under fourth toe 22-27, entire or proximally divided. Palms and soles smooth or weakly tuberculate.

In adults and subadults, black laterodorsal stripe usually wider than in *E. w. tenebrosa*, ragged-edged and enclosing less regular white spots (which are sometimes very reduced in size and sometimes coalescing into lines). Sides of body stippled heavily with black and sparsely with white. Upper surface of tail stippled with black. Black facial streaks well developed, viz.

one from nostril back, immediately below eye, to top of ear aperture and a little beyond; another and higher, branching from first streak in front of eye and extending back to temples; and often a third, still higher, back from eye to side of neck. Prominent white subocular streak from below nostril back (or almost so) to lower half of ear aperture, posteriorly margined below by black streak along bottom of upper labials. Under surface greyish white, except on throat, which may have dark sutures between chin-shields or scattered black blotches or greyish smudges.

Remarks.—The type of *whitei* was collected before the penetration of the Blue Mountains and probably came from Sydney, where John White resided between 1788 and 1793.

The syntypes of *moniligera* could have come from both Sydney and the Blue Mountains (Péron, for one, visited both). Duméril & Bibron's name (meaning necklace-bearing) is more apt for the Blue Mountains form than *adult* Sydney lizards. However, the animal whose measurements they give is far larger than any Blue Mountains specimen I have seen and almost certainly came from Sydney.

A specimen (NM 7864) said to come from Blackheath (Blue Mountains) is best identified with *E. w. whitei*. It has a snout-vent length of 97 mm and coloration very like that of the Kurnell specimen except that its white subocular streak is poorly developed. Blackheath is only 11 miles southeast of Hartley, from which there are long series of *E. w. tenebrosa*.

Material.—*New South Wales*: Grafton (NM 3458), Coast Range (NM 3459), Hunter River (NM 918), Sydney (NM 4174; NTM 2764, 2774), Randwick (AM 4038, 4040-1; NM 2760-1; WAM 14475), North Botany (AM 4170), Botany (AM 18487), Kurnell (NM 8885), Waterfall (AM 15123, 18772).

Egernia whitei modesta subsp. nov.

Holotype.—J 464 in Queensland Museum, an adult collected on 12 November 1912 at Chinchilla, Queensland.

Diagnosis.—A large, long-tailed, short-limbed subspecies of *E. whitei* in which adults have little or no colour pattern. Nasals narrowly separated. Tubercular calli on proximal subdigital lamellae.

Distribution.—Southeastern interior of Queensland north to Eidsvold and west nearly to St. George. Northeastern interior of New South Wales from Tenterfield south and west to Narrabri.

Description.—Head and body moderately depressed. Ear aperture moderately narrow to wide; lobules 2-5, acute or obtuse or serrate, usually decreasing in size downwards. Snout-vent length (mm): 44-112. Length of appendages (% SVL): foreleg 23-33, hindleg 33-43, tail 151-177.

Nasals narrowly separated, seldom touching. Prefrontals forming a short to long median suture, seldom separated. Frontal much wider than interparietal in adults, slightly wider in juveniles. Supraciliaries 7-9 (mostly 7 or 8). Upper palpebrals 10-14. Upper labials 7-9

(mostly 8). Midbody scales smooth; 33-40 rows. Lamellae under fourth toe 21-26, compressed, proximally divided and tuberculately callose, distally entire and smooth or weakly callose.

Only smallest juveniles have characteristic *whitei* pattern (back striped, sides ocellate). Pattern in large juveniles and subadults reduced or absent. Back and sides of adults uniformly olive; tail pale brown; under surface greyish white.

Paratypes.—*Queensland*: Eidsvold (AM 5314), Gayndah (AM 5535-6), Chinchilla (QM 13207-13), Greymare, near Thane (QM 13366), Thormby Station, E. of St. George (QM 3825). *New South Wales*: Tenterfield (AM 2894), Moree (AM 1824), Narrabri (AM 1059). No locality: AM 5014-6.

Egernia whitei tenebrosa

Egernia whitei tenebrosa Condon 1941, Rec. S. Aust. Mus. 7: 111. Flinders Chase, Kangaroo Island, South Australia.

Diagnosis.—A small, brownish subspecies of *E. whitei* which undergoes no ontogenetic change in coloration. Colour pattern (when present) more sharply defined than in other subspecies. No prominent white subocular streak. Tail usually unmarked.

Distribution.—Eastern interior of New South Wales: the Great Dividing Range and associated mountains from Point Lookout and the Warrumbungle Range south to the Monaro Tableland and Australian Alps, inland on western slopes to Mudgee and Cootamundra. Southern Victoria north to the Great Dividing Range; Lady Julia Percy Island. Bass Strait Islands: King Island, Kent Group and Furneaux Group (The Sisters, Flinders and Hummock Islands). Tasmania: northern and eastern lowlands and hills (up to 1200 feet) from Table Cape east to Gladstone and south to Hobart; islands off north coast (Three Hummocks, Waterhouse and Swan). South Australia: the southeast north to the Coorong and Penola; Mt. Lofty Range; Yorke Peninsula; Wedge Island; Kangaroo Island.

Description.—Head and body slightly depressed. Appendages moderately long in north, usually short in south. Ear aperture wide to moderately narrow; lobules 2-5, acute or obtuse, usually decreasing in size downwards. Snout-vent length (mm) 32-101 (90 seldom attained except in far north and on islands). Length of appendages (% SVL): foreleg 21-33, hindleg 30-48, tail 120-183.

Nasals widely or narrowly separated. Prefrontals separated or forming median suture. Frontal usually much wider than interparietal in adults; slightly wider or slightly narrower in juveniles. Supraciliaries 5-9. Upper palpebrals 8-13. Upper labials 7-9. Midbody scales smooth (sometimes tristriate); 30-43 rows. Lamellae under fourth toe 16-27, proximally divided and callose, distally entire and smooth or feebly callose. Palms and soles smooth.

Some individuals ("plain-back") have no dorsal pattern, and others ("patternless") neither dorsal nor lateral markings; but most have a bold clear-cut pattern of dorsal stripes

and lateral ocelli. Dorsal ground colour greyish brown to rufous brown, more olive on head, clearer and paler brown on tail. Broad, black, sharp-edged laterodorsal stripe enclosing single row of white spots (which anteriorly may coalesce). Pattern on flanks sharply demarcated from grey dorsolateral stripe and consisting of white, black-edged spots, which on side of shoulder form a short, white, black-edged bar (sometimes broken) extending from insertion of arm up to dorsolateral stripe. Tail usually unpatterned. Dark facial stripes not so well developed as in nominate race. Pale subocular streak obscure or absent. No dark labial streak. Under surface pale grey.

Geographic variation.—Wherever these skinks are abundant and more or less continuously distributed (as from the Blue Mountains south through Bass Strait to Tasmania) there is little variation in size and coloration, and scale counts and proportions only change gradually. Where the populations are isolated (as in the north and west) or restricted to small areas (as on Lady Julia Percy Island) there are apt to be large and unpredictable departures from normal, especially in size and coloration.

Generally body-size, relative length of appendages, scale counts and size of prefrontals decrease from north to south. But, as the following analyses show, clines terminate more often on the Victorian mainland than in Tasmania.

Maximum snout-vent length in most populations is 85-91 mm. In the lower north of New South Wales 96 is attained at Barrington Tops and 95 in the Mudgee district. Lady Julia Percy Island lizards are anomalously large (up to 97). However the largest *tenebrosa* I have seen is one from Upper Yarra with SVL 101, i.e. 11.5 mm more than any other specimen from the Victorian mainland.

The tail is relatively longest in New South Wales, population averages for adults varying between 160 and 170% of SVL. In South Australia (including Kangaroo Island) and Bass Strait it averages 150-160; in Victoria (including Lady Julia Percy Island) and Tasmania (including Waterhouse Island) 140-150. Relative length of foreleg in adults is greatest in the Warrumbungle and Mt Lofty Ranges (28-29%); on Kangaroo and the Bass Strait Islands it averages 27-28; in most of New South Wales 26-27, and in Victoria and Tasmania 25-26. Relative length of hindleg in adults averages 39-40% in the lower north of New South Wales, South Australia and Bass Strait Islands; 37-38 in southern New South Wales and on Lady Julia Percy and Kangaroo Islands, 36-37 in central New South Wales and Tasmania, and 35-36 on the Victorian mainland.

Midbody scale-rows average 41 in the Warrumbungles, 35-37 in the remainder of New South Wales, 34-36 in South Australia and on Lady Julia Percy Island, and 33-34 in Victoria, Bass Strait and Tasmania. Subdigital lamellae under fourth toe average 22-24 in the lower north of New South Wales, 22-23 in central and southern New South Wales and on Kangaroo Island, 21-22 on the South Australian

mainland and Bass Strait Islands, 20-21 on Lady Julia Percy Island and Tasmania, and 19-20 on the Victorian mainland.

On Kangaroo Island counts of 8 upper labials are much more frequent than 7. In Tasmania and central and southern New South Wales counts of 8 are as frequent as 7, but in the remainder of the subspecies' range 7 is much more frequent than 8.

Palpebral counts average 12 in the Warrumbungles, about 11 in the remainder of New South Wales, between 10 and 11 in Bass Strait, Tasmania and South Australia and a little less than 10 in Victoria. Supraciliaries average between 7 and 8 in the lower north of New South Wales, about 7 in central and southern New South Wales and between 6 and 7 in the remaining populations.

No specimen from the lower north of New South Wales has the prefrontals separated. In central and southern New South Wales 5% of specimens have them separated, on the Victorian mainland 10%, South Australian mainland 15%, Kangaroo Island 17%, Lady Julia Percy Island (just off the Victorian coast) 24%, Bass Strait Islands 47%, Waterhouse Island (just off the north coast of Tasmania) 57%, and Tasmania 78%.

It now remains to mention some non-clinal variation. Populations from the lower north of New South Wales vary considerably in size, meristics and coloration, which indicates their isolation from each other. The three specimens from the Warrumbungles are the most distinctive. Their limbs are very long in contrast to the extremely short limbs of *E. w. modesta*, which occurs at Narrabri only 75 miles to the north. The largest of the Barrington Top series have a reddish suffusion on the fore-back, which together with their large size and some development of dark tubercles on soles, suggests introgression from nominate *whitei*.

The skinks from Hartley in the Blue Mountains are generally very like those from southern New South Wales, Victoria and Tasmania. Their only peculiarity is the high number of ear lobules.

Kangaroo Island skinks are very variable in coloration. They are generally browner than elsewhere, and the variants "plainback" and "patternless" are moderately common. Almost all specimens have 8 upper labials.

The most distinctive population of *tenebrosa* is that occurring on Lady Julia Percy Island off the coast of western Victoria. As well as being large, many of these skinks have the tail and flanks stippled with black as in nominate *whitei*. Even the belly may be spotted. However most of the island colour variants, including "plainback" and "patternless", can be matched fairly well with odd specimens from the mainland of Victoria, especially the Grampians and their vicinity.

Material.—New South Wales: Point Lookout (AM 17136-8), Tubrabucca, Barrington Tops (AM 13344-9; NM 7833, 7922), Warrumbungle Range (AM 14970-2), Guntawang (AM 4044), Rylstone (AM 15358), Portland (AM 1555), Hartley (AM 1314-32, WAM 14474), Cootamundra (AM 792), Mt Kosciusko 3000 feet

(AM 5224-5), Bombala and Snowy Range (AM 4709, 5729-30, 11669). *Australian Capital Territory*: near Gasuk Gap (WAM 13369), no (AM 485-6, 492-9, 507-10, 5693, 5700), Berridale precise locality (AM 12497-9). *Victoria*: Buchan (NM 1671), Rosedale (NM 2499, 2500), Wilsons Promontory (NM 8112), Schnapper Point (NM 5898-9), Mordialloc (NM 4184), Upper Yarra (NM 1089), Mt Dandenong (NM 2896), Ringwood (NM 2878, 5563), Caulfield (NM 5494-5), Prahran (NM 1825), Coburg (NM 1047), Keilor (NM 2724-32, 5642-6), Sunbury (NM 951, 4170-3), Beaufort (NM 1612), Ararat (NM 2219), Stawell (NM 1233, 3457), Grampians including Mt William (NM 927, 2240-2; SAM 3194, 8567-8), Byaduk (NM 1507-10), Drumborg (NM 7927), Nelson (SAM 1146), Lady Julia Percy Island (AM 11750-1; NM5301-9, 8055-6, 10945-51; WAM 9885-7), no precise locality (NM 1191-2; AM 4126). *Bass Strait Islands*: King Island, including Narracoopa (AM 3658; NM 2145, 2626-7), Kent Group (NM 3454-6), West Sister Island (AM 12284), East Sister Island (AM 12282), Flinders Island including Emita and Killicrankie Bay (AM 12285, 14447; NM 11734-5; QVM a-b); Hummock or Prime Seal Island (NM 11748), "Bass Straits" (AM 4043). *Tasmania*: "Two Hummocks Island" (NM 13168-70), Waterhouse Island (QVM a-g), Swan Island (NM 30), Gladstone (QVM a-j), Nabowla (QVM a), Greens Beach (QVM a-c, SAM 6598), Launceston (AM 6757, QVM a-d), Trevallyn (QVM a-c), Cataract Gorge (QVM 1026), Tunbridge (QVM a-b), Lake Sinclair (SAM 8501), Freycinet Peninsula (WAM 28483-4), no precise locality (AM 2052, 5698-5706, 6759-61; NM 980, 2091, 2099; SAM 2895 a-c). *South Australia*: Penola (SAM 8560), South Coorong sandhills (SAM 2896, 8457), Tapanappa (SAM 2828), Basket Range (SAM 1649), Bulls Creek (SAM 7582), West Island, Encounter Bay (SAM 1696), Cape Jervis (SAM 7722-4), Yorke Peninsula (SAM 2897), Wedge Island (SAM 574, 5348, 8504). *Kangaroo Island*: Flinders Chase (SAM 2665), Ravine des Casoars (SAM 3278, 8475-7), American River (WAM 16794-7), Birchmore Lagoon (AM 7131), Deep Creek (AM 7153-4), no precise locality (SAM 794, 1185, 2904, 2907, 3478, 5926, 8456, 8458-67).

Egernia multiscutata multiscutata

Egernia whitii multiscutata Mitchell & Behrndt 1949, Rec. S. Aust. Mus 9: 176. Greenly Island, South Australia.

Diagnosis.—The species *multiscutata* is a small long-limbed member of the *E. whitei* species-group, most like *whitei* but differing in its much wider interparietal, bicarinate subdigital lamellae and laterodorsal stripe usually enclosing two series of pale spots.

Distribution.—Greenly Island, off southwest coast of Eyre Peninsula, South Australia.

Description.—Head and body slightly depressed. Ear aperture narrow to moderately wide; lobules 3 or 4, obtuse, subequal or slightly decreasing in size downwards. Snout-vent length (mm) : 50-88. Length of appendages (% SVL) : foreleg 30-34, hindleg 44-47, tail 152-168.

Nasals widely or narrowly separated, occasionally forming short median suture. Prefrontals

forming a short to long median suture, sometimes narrowly separated. Frontal a little wider or narrower than interparietal in adults, much narrower in juveniles. Loreals 2, second usually a little lower than wide. Supraciliaries 6-8 (mostly 7). Upper palpebrals 8-11. Upper labials 8. Midbody scales smooth, 40-46 rows. Lamellae under fourth toe 22-26, with two widely separated series of keels.

Dorsal ground coloration dark brown or brownish grey. Black laterodorsal stripe (much broader than pale vertebral stripe) enclosing two series of pale spots or short longitudinal lines. Head olive grey or brown variegated with black. Tail dappled with black or dark brown. No pale dorsolateral stripe. Sides of body speckled heavily with black and sparsely with white. Chin-shields and posterior labials broadly margined with black or dark grey. Throat suffused with grey. Under digits dark horn-colour. Remainder of under surface pale bluish grey.

Remarks.—The species *E. multiscutata* undergoes hardly any more geographic variation than the subspecies *tenebrosa* of *E. whitei*; thus the propriety of subdividing it is not yet certain. The typical population happens to be the most distinctive in ecology, morphology and coloration.

Material.—*South Australia*: Greenly Island (type series—SAM 2636 a-e, 8579-81).

Egernia multiscutata bos

Egernia bos Storr 1960, W. Aust. Nat. 7: 99. Cheyne Beach, 32 mi. E of Albany, Western Australia.

Diagnosis.—Distinguished from *E. m. multiscutata* by paler coloration, presence of pale dorsolateral stripe, deeper head and body, and shorter limbs (especially hindleg).

Distribution.—Subhumid and semiarid sandplains and coastal dunes of southwestern and southern Australia. Western Australia from Bernier Island (Shark Bay) to Israelite Bay, inland to the Midland sandplains and Eastern Goldfields but excluding the wet southwest corner south of Lancelin and west of Cheyne Beach; Jurien Bay islands. South Australia: west coast of Eyre Peninsula, St. Francis Island, Thistle Island, Yorke Peninsula and Kangaroo Island.

Description.—Head and body usually deep. Ear aperture narrow (often slit-like); lobules 3-5 (mostly 4), usually obtuse (occasionally squarish or acute), usually subequal, sometimes decreasing slightly in size downwards. Snout-vent length (mm): 34-94. Length of appendages (% SVL): foreleg 24-35, hindleg 34-47, tail 126-179.

Nasals widely or moderately separated (seldom narrowly). Prefrontals forming a median suture (seldom narrowly separated). Frontal a little wider or narrower than interparietal in adults, much narrower in juveniles. Loreals 2, second usually a little higher than wide. Pre-suboculars usually 2, seldom 3. Supraciliaries 6-9 (mostly 8). Upper palpebrals 8-14. Upper labials 7-9 (mostly 8, seldom 9). Midbody scales smooth, 37-46 rows. Lamellae under fourth toe 21-27, usually bicarinate.

Dorsal ground coloration pale grey or brown, becoming olive on head. Black laterodorsal stripe usually present, no wider or not much wider than pale vertebral stripe, enclosing two (locally one) series of pale spots or short longitudinal lines. Pale dorsolateral stripe. Sides of body usually suffused (rarely marbled) with pale greyish brown (becoming blackish on scale sutures) and occasionally spotted with white. Black spots on tail usually arranged in transverse rows. Posterior labials narrowly margined with black. Chin-shields occasionally with narrow dark grey margins. Under digits pale horn-colour. Remainder of under surface pale bluish grey.

Geographic variation.—Like its distribution, variation in *bos* is generally disjunct rather than continuous. However, a few clines can be observed in Western Australia. From Bernier Island south through Jurien Bay and the Wheat Belt to the south coast, mean number of mid-body scale-rows increases from 39.5 to 42.2, subdigital lamellae decrease from 25.5 to 23.2, relative length of tail decreases from 167 to 138% and hindleg from 43.4 to 39.7%.

The typical population (south coast sandplains from Cheyne Beach to Israelite Bay) is one of the most distinctive. These skinks are pale and short (SVL not greater than 82) and have an extremely deep head and body and high foreleg-hindleg ratio (78%).

In the central and southern Wheat Belt of Western Australia, coloration is darker and browner, the head and body not so deep, and the foreleg-hindleg ratio lower (73%). West coast skinks are generally similar, though larger and longer-tailed. In the southeastern interior of Western Australia (from Lake Varley northeast to Coonana) the black laterodorsal stripe is narrow and the outer series of pale spots usually lost.

Reduction of the laterodorsal stripe is carried much further in South Australia. In the single specimen from Mt. Wedge the outer series of pale spots is disappearing. Two of four specimens from Point Fowler have no laterodorsal stripe, and the single adult from Thistle Island is almost patternless.

The remaining South Australian populations are more normally coloured. Skinks from St. Francis Island are especially similar to typical *bos*. They are identical in coloration and habit but are a little larger (SVL up to 90) and have relatively longer appendages and more numerous midbody scale-rows, subdigital lamellae, upper labials, upper palpebrals and supraciliaries.

Material.—*Western Australia*: Shark Bay islands—Bernier (WAM 13118-9, 20498-20504); Jurien Bay islands—Sandland (WAM 16808-13), Favourite (WAM 16798-16800), Boullanger (WAM 16801-2), Essex (WAM 16803-7); South-West Division—Stockyard Gully (WAM 26746), Mt. Lesueur (WAM 22235-6), Lancelin Island (WAM 16814-20), 16 mi. W of York (WAM 16821), Boyagin (WAM 18546), 16 mi. E of Pingelly (WAM 16822-3), Corrigin (WAM 12646), Lake Varley (WAM 19241, 26177), Ongerup (WAM 2535), Toolbrunup (WAM 1384), Cheyne

Beach (WAM 10752-4, 16824-38); Eastern Division—8 mi. W of Coonana (WAM 16843-4), between Queen Victoria Spring and Fraser Range (SAM 2900); Eucla Division—20 mi. N of Cape Arid (WAM 16839-40), 15 mi. SW of Israelite Bay (WAM 16841-2), Israelite Bay (WAM 17624-5). *South Australia*: Eyre Peninsula—Point Fowler (SAM 5761, 5765, 8498-9), St. Francis Island (SAM 2902-3, 2905-6, 8451-4, 8468-74), Mt. Wedge (SAM 5764), Elliston (SAM 5746), Fishery Bay (SAM 2549 a-b), Thistle Island (SAM 2547, 8582); Yorke Peninsula—Sweat Island (SAM 2901); Kangaroo Island—Birchmore Lagoon (AM 7129), no precise locality (SAM 8465).

Egernia inornata

Egernia inornata Rosén 1905, Ann. Mag. Nat. Hist. (7) 16: 139. "West Australia" (Holst).

Diagnosis.—A small member of the *Egernia whitei* group with moderately short snout, deep head and short tail; back yellowish or reddish brown, immaculate or spotted with black; spotting denser on sides and arranged in irregular vertical bars; spotting on top and sides of tail arranged in narrow transverse bars. Distinguished from *E. striata* and *kintorei* by presence of black pigment, and from *E. slateri* by absence of pale bluish-grey on ventral surfaces.

Distribution.—Arid and semiarid extratropical interior of Australia: Western Australia from Merlinleigh (100 mi. ENE of Carnarvon) and 40 mi. NW of Warburton Range south to the northeastern and eastern fringes of Wheat Belt (Jibberding, Wialki and 40 mi. E of Narembene), Eastern Goldfields and southern edge of Great Victoria Desert; Northern Territory north to the Ehrenberg Range, Haasts Bluff and Todd River Station; South Australia south to central Eyre Peninsula (Hambidge Reserve) and Murray Mallee; New South Wales at Nymagee in central west.

Description.—Body robust, not depressed. Ear aperture narrow, sometimes moderately wide; lobules 3-6 (mostly 4, seldom 5 or 6), white, usually small and obtuse, subequal or slightly decreasing in size downwards. Snout-vent length (mm): 32-84; smallest male with everted hemipenes 56. Length of appendages (%SVL): foreleg 24-35, hindleg 32-45, tail 108-148.

Nasals widely or narrowly separated, rarely touching or forming very short median suture; groove representing nasal-postnasal suture usually discernible. Second loreal usually a little higher than wide. Presuboculars 2, rarely 3; first occasionally fused to second loreal. Prefrontals usually forming a median suture, occasionally just touching or narrowly separated. Frontal a little wider or narrower than interparietal. Supraciliaries 5-9 (mostly 7 or 8). Upper palpebrals 9-14. Upper labials 7, rarely 6 or 8. Midbody scales smooth, 34-42 rows. Lamellae under fourth toe 19-28, proximally notched (occasionally entire or divided), usually with an apical series of weak or strong calli, sometimes smooth or bicallose.

Dorsally yellowish brown, fawn or coppery red, tending to olive grey or brown on head. Back immaculate or spotted with black; spots tending to be elongate and longitudinally

aligned. Upper lateral spots more numerous and conspicuous, longitudinally elongate but irregularly aligned into transverse bars slightly deflected forwards inferiorly. Caudal spots most prominent dorsolaterally, but usually enough on upper surface to form more or less continuous, narrow bands. Under surface pinkish or creamy white.

Geographic variation.—Dorsal coloration is more yellowish in southern semiarid habitats and more reddish in northern habitats. Geographic variation in meristics and proportions is small, unpredictable and local rather than clinal, which suggests some slight regional constriction in gene-flow.

Central Australian specimens have a shorter tail (119.9% of SVL) and hindleg (37.4) than average, and fewer subdigital lamellae (22.2) and upper palpebrals (10.1). Specimens from the Musgrave region, about 200 miles to the southwest, have a longer-than-average hindleg (38.2), fewer midbody scale-rows (36.6), and more subdigital lamellae (24.5) and upper palpebrals (11.4). A further 3-400 miles to the southwest, in the western parts of the Great Victoria Desert, the skinks are larger than average (they alone include specimens with SVL greater than 79 mm) and have a longer tail (132.2) and shorter-than-average foreleg (27.9).

Remarks.—The type of *inornata* was among a collection of nine species made by the Swedish geologist Dr N. Holst in 1896-7. There is only one area where all these nine species occur together, namely the Kalgoorlie-Leonora-Laverton region. The Lund Museum was unable to precise the locality of Holst's specimens or give me details of his itinerary except that "it appears from a letter . . . that he, for some time, visited Kalgoorlie".

Material.—*Western Australia:* North-West Division—Merlinleigh (WAM 8601); South-West Division—15 mi. E of Jibberding (WAM 28265), Wialki (WAM 16845), Merredin (WAM 1268), 40 mi. E of Narembeen (WAM 25992); Eastern Division—40 mi. NW of Warburton Range (WAM 14639-42), 30 mi. NW of Warburton Range (WAM 15144), Warburton Range (WAM 22104-6), Gahnda Rockhole (WAM 19977), Albion Downs (WAM 25066), 12 mi. N of Coolgardie (WAM 16846-7), Dedari (WAM 14120 a-c), 40 mi. NW of Cundeelee (WAM 13038), 12 mi. NW of Cundeelee (WAM 13041), Queen Victoria Spring (WAM 13028, 16849-52), 12 mi. S of Queen Victoria Spring (WAM 12243), near Lake Ell (WAM 16853-5), plus 57 specimens in Dr Pianka's collection from 17 mi. S of Atley, 5 mi. W of Lake Yeo Out-Station, 111 mi. W and 18 mi. S of Neale Junction, etc.; Eucla Division—Smithania Rock (WAM 25511). *Northern Territory:* Ehrenberg Range (JSE 364-5, 391), 30 mi. W of Haasts Bluff (AM 21110), Alice Springs District (AM 25794), Todd River Station (NTM 1448-52, 1465, 1503, 1528-35, 1890-6, 2536-51, 2553-4, 2557-74), Allambi Station (NTM 2552, 2555-6), Numery (NTM 2820), Deep Well (NTM 2636), Palmer Valley Station (NTM 1540), Curtin Spring (JSE 11, 39). *South Australia:* Musgrave Park (SAM 7209-66, 7681-5), Immarna (SAM 1024), Hambidge Reserve (SAM 8934), Yudnapinna (SAM

3041, 3057), Tinga Tingana (SAM 754), Tallaringa Well (SAM 5533), Mt. Burrell Station (SAM 294, 8421-9), Renmark (NTM 2755-6), Turners Well (SAM 22), Purnong (SAM 1024). *New South Wales:* Nymagee (AM 15331, 15334, 17894, 18476).

Egernia slateri slateri subsp. nov.

Holotype.—R 29130 in the Western Australian Museum, formerly NTM 2051, an adult male collected by D. A. Lindner and K. R. Slater on 3 September 1964 at Alice Springs, Northern Territory, in 23° 46' S, 133° 53' E.

Diagnosis.—A moderately small but robust member of the *E. whitei* group with short snout, deep head and greyish brown back spotted with dark brown or black. Intermediate in size and meristics between *E. striata* and *inornata* but distinguished from both those species by its pale bluish-grey venter and lack of reddish pigments. Further distinguished from *striata* by its much wider pupil and presence of black pigment and from *inornata* by its white-flecked lateral scales.

Distribution.—Alluvial plains in the valleys of the major Central Australian rivers (the Todd, upper Finke and upper Palmer) from Alice Springs southwest to Tempe Downs.

Description.—Body not depressed; ear aperture narrowly rectangular or elliptical; lobules 4-6 (mostly 4), white, usually obtuse (sometimes acute, especially superiorly), subequal or with lowest largest and second-lowest smallest. Snout-vent (mm) 38-93; smallest male with everted hemipenes 65. Length of appendages (% SVL); foreleg 24-34, hindleg 33-45, tail 113-144.

Nasals usually widely, sometimes narrowly, separated; groove representing nasal-postnasal suture usually faint. Prefrontals forming a long or short median suture, rarely separated. Frontal slightly wider than interparietal, seldom narrower. Loreals normally 2, second usually higher than wide. Presuboculars normally 2, first occasionally fused with second loreal. Supraciliaries 7 or 8 (rarely 6 or 9). Upper palpebrals 11-16. Upper labials usually 7, occasionally 8, rarely 6. Midbody scales smooth, striate, 37-44 rows. Lamellae under fourth toe 19-27, usually entire (sometimes basally notched, rarely divided), with a single apical series of dark, weak, obtuse keels (occasionally an additional series on basal lamellae).

Head iridescent olive grey-brown. Back greyish brown, many scales with outer third black or dark brown, the resultant spots forming more or less distinctly longitudinal stripes. Dorsolaterally and laterally, dark lateral edges of scales not so prominent as narrow whitish or pale brown posterior edge. Tail pale brown spotted with black and dark brown; spots irregularly shaped and tending to align longitudinally on upper surface and transversely on sides. Upper surface of limbs pale rufous brown with more or less distinct darker longitudinal stripes. Eyelids blackish except for creamy margin of free edges. Posterior upper labials (and sometimes posterior lower) more or less broadly margined with black or dark brown. Throat, chest and belly pale bluish; under limbs and girdles yellowish white.

Geographic variation.—All but one specimen come from two localities, Alice Springs and Hermannsburg. Though only 65 miles apart, these populations differ slightly in several characters. Hermannsburg skinks have longer limbs, fewer midbody scale-rows (38 slightly more frequent than 40, whereas 40 is considerably more frequent than 38 at Alice Springs) and fewer supraciliaries (7-9 with 8 more frequent than 7, against 6-8 with 7 overwhelmingly dominant at Alice Springs).

Remarks.—This skink is named after K. R. Slater who was first to demonstrate its morphological and ecological distinctiveness. Mr Slater kindly donated the holotype to the Western Australian Museum.

Paratypes.—*Northern Territory*: Alice Springs (NTM 2052-62, 2169, 2171, 2191-3, 2195, 2197-8, 2200, 2227-31, 2269, 2272-4, 2286-97, 2299, 2300, 2605, 2683-6, 2757, 2853, 2883), 5 mi. S of Alice Springs (WAM 24427-31), 10 mi. NE of Hermannsburg (NTM 2348-50, 2578, 2604, 2606, 2634), Tempe Downs (NTM 2771).

Egernia slateri virgata subsp. nov.

Holotype.—R 602 in South Australian Museum, an adult collected by S. A. White between Oodnadatta and the Everard Range, South Australia.

Diagnosis.—Distinguished from *E. s. slateri* by conspicuous black vertebral stripe.

Distribution.—Far northern South Australia.

Description.—Similar in habit to nominate *slateri*. Ear aperture narrow in adult, much wider in juvenile; lobules 4 or 5, obtuse. Snout-vent length of adult 94, of juvenile 50.

Nasals moderately separated. Prefrontals just touching or forming short suture. Frontal as wide as interparietal in juvenile, a little wider in adult. Loreals 2, second as high as wide or higher. Presuboculars 2. Supraciliaries 8 or 9. Upper palpebrals 12. Upper labials 7. Midbody scales smooth, 40 rows. Lamellae under fourth toe 22-24, slightly compressed, entire or basally divided, with an apical series of weak calli.

Prominent blackish vertebral stripe from occiput to at least base of tail. A broken blackish laterodorsal stripe. Sides with dark spots or short longitudinal bars, mixed (in juvenile) with small obscure whitish spots. Posterior labial sutures broadly or narrowly margined with black or dark brown. Under surface unmarked.

Remarks.—The exact provenance of the holotype is unknown. It was evidently collected by Capt. White in June or July 1914 during his trip to the Everard Range (White 1915) and is almost certainly one of the three specimens listed by Zietz (1915) under "*Egernia whitii*" as coming from Oodnadatta, Wantapella and the Musgrave Range. Only the second of these localities could be described as "between Oodnadatta, and the Everard Range." Wantapella is a lignum swamp 5 miles southwest of Granite Downs.

The paratype (D 273 in National Museum) is a juvenile collected by W. Baldwin Spencer. Though registered as "Central Australia, 1896" it may have been collected by the Horn

Expedition. At any rate Lucas & Frost's description (1896:138) of three "*Egernia whitii*" from Oodnadatta and their fig. 3 (pl. XI) could only have been based on examples of *virgata*.

Egernia striata

Egernia striata Sternfeld 1919, Senckenbergiana 1: 79. Hermannsburg, Northern Territory (M. von Leonhardi).

Diagnosis.—A moderately large member of the *E. whitei* species-group with short deep head, vertically narrow pupil, short tail, strong limbs, and reddish-brown back with darker longitudinal stripes. Most like *E. kintorei* from which it can be distinguished by its unique pupil-shape, much smaller size, fewer midbody scale-rows and upper labials, lower second loreal and longer and sharper ear lobules. Distinguished from *E. inornata* and *E. slateri* by absence of black markings.

Distribution.—Arid zone of Australia: Western Australia from Woodstock (Pilbara) and Godfreys Tank (Great Sandy Desert) southeast to Laverton and Neale Junction (Great Victoria Desert); Northern Territory north to the Smoke Hills (Tanami Desert) and Tennant Creek; and far northwestern South Australia.

Description.—Body stout, not depressed. Head very short and wide but not quite so deep as in *E. kintorei*. Ear aperture usually narrow; lobules 3-6 (mostly 4 or 5, very rarely 3), obtusely or acutely triangular (rarely rectangular as in *kintorei*), subequal or slightly decreasing in size downwards. Snout-vent length (mm): 41-117; smallest male with everted hemipenes 82. Length of appendages (% SVL): foreleg 23-40, hindleg 29-47, tail 105-146.

Nasals widely separated (very rarely narrowly separated). Prefrontals usually forming a long median suture, seldom separated. Frontal a little wider or narrower than interparietal. Loreals normally 2, second 0.7-1.7 (1.1) times as high as wide. Presuboculars usually 2 (3 in only 9% of specimens). Supraciliaries 7-11 (usually 8 or 9, very rarely 11). Upper palpebrals 10-16. Upper labials 6-8 (mostly 7, very rarely 6), third-last occasionally precluded from orbit by enlarged palpebrals. Midbody scales smooth, 36-46 rows (seldom fewer than 38 or more than 44). Lamellae under fourth toe 17-25, proximally notched or divided; an apical series of weak and pale or strong and dark calli.

Back fawn or reddish-brown with obscure or pronounced longitudinal stripes caused by darkening of lateral edges of scales. Stripes extending forward to neck and backwards to base of tail, becoming broken on sides, finally disappearing or degenerating into more or less transverse rows of spots. Lateral ground coloration gradually changing from reddish brown to pale greyish-brown and finally greyish white (in contrast to *kintorei*, colour of flanks generally paler than back and not so sharply demarcated). Labials whitish, the posterior margined broadly with reddish or dark brown. Under surface white.

Geographic variation.—In this abundant and widespread skink geographic variation is slight, and only a little of it seems to be clinal. Ani-

imals from the northern half of the range (i.e. north of the Tropic) are a little larger than southern animals and have relatively shorter appendages. Maximum snout-vent length varies between 117 (Smoke Hills, N.T.) and 104 (Laverton, W.A.). Mean relative length of tail in adults varies between 117 and 125 in northern populations, against 119-129 in the south. The corresponding data for foreleg and hindleg are 25-26 (26-28) and 32-34 (34-37).

In the centre of the species' range, i.e. far northwest of South Australia, far east of Western Australia (Warburton Range) and southwest of the Northern Territory (Kintore Range), the frequency of specimens with frontal narrower than interparietal is about 10%; elsewhere it is about 50%. In the northeast (Tanami to Hermannsburg) the mean frequency of specimens with 3 suboculars is 22%, compared to only 4% in the remainder of the range.

Variation in all other scale characters is minor and local. Mean number of midbody scales varies from 39.4 in the Kintore Range (N.T.) to 42.3 at Laverton (W.A.); lamellae, 20.1 (Reedy Creek, N.T.) to 22.4 (Kintore Range); upper labials, 7.0 to 7.2; upper palpebrals, 11.6 (Laverton) to 14.2 (Hermannsburg); supraciliaries, 8.0 (Corandirk, N.T.) to 9.0 (Hermannsburg); and ear lobules 4.3 (Musgrave Park, S.A.) to 5.1 (Corandirk and Aileron, N.T.).

There is generally less geographic variation in colour than individual variation, though some populations could be classified as darker, redder and more strongly striped than others. The most distinctively coloured population is that from the far northeast (between Tennant Creek and Wauchope, N.T.). These skinks have only the vertebral and paravertebral stripes well developed; the remaining dorsal stripes are more or less broken.

The foregoing remarks and descriptions do not include a peculiar specimen (WAM 13027) from 60 miles east of Kalgoorlie, Western Australia. This skink is coloured exactly like *E. kintorei* (i.e. dorsum pale pinkish-brown, faintly striped; sides clear grey) but agrees with *E. striata* in its small size (SVL 100), low number of midbody scale-rows (41), low number of upper labials (7), and triangular ear lobules. A decision on the systematic position of this population (the only one of the *kintorei-striata* complex known to occur south of the "Mulga-Eucalypt Line") awaits the collection of more specimens and especially information on pupil-shape, ecology and maximum size.

Remarks.—Sternfeld's original description of *striata* is fairly complete, but he did not mention *inornata* or *kintorei*, let alone show how to distinguish *striata* from them. In 1924 he compared *striata* with *whitei* but not with either of its close relatives. It is little wonder then that Loveridge (1934) synonymised *striata* with *inornata*. Though Mitchell (1950) established the distinctness of *kintorei* from *inornata*, it remained for K. R. Slater (after studying the complex in the field) to rescue *striata* from oblivion.

Meanwhile Mertens (1922 : 174) had selected a lectotype from Sternfeld's 11 syntypes of *striata*. Recently Professor Mertens kindly sent me a photograph of this specimen, which has assured me that Sternfeld's name is correctly applied to the present taxon.

Material.—*Western Australia:* North-West Division; Woodstock (WAM 13088-9, 13455), Turee Creek (WAM 25136-7); Eastern Division—Godfrey's Tank, Canning Stock Route (WAM 4001, 4003), 178 mi. E. of Carnegie (WAM 28809-12), Warburton Range (WAM 15145, 17108-9, 17779, 22005, 22113, 22134, 22208-10, 24837), Nullye Rockhole, 110 mi. ENE of Cosmo Newbery (WAM 16856), 64 mi. ENE of Cosmo Newbery (WAM 28870), Kathleen Valley (WAM 27227), plus 76 specimens in Dr Pianka's collection from 10 mi. N of Millrose, 24 and 110 mi. ENE of Laverton, 80 mi. W and 16 mi. S of Neale Junction etc. *Northern Territory:* Smoke Hills, 30 mi. E of Tanami (NTM 2780-2), Tanami Desert Sanctuary between 20° 26' and 20° 58' S, in 130° 41' E (NTM 2783-4), 20 mi. E of The Granites (WAM 25378-25404), Corandirk, ca 80 mi. SE of The Granites (NTM 2611, 2629, 2631, 2650-8), 15-38 mi. S of Tennant Creek (WAM 21459-61), Aileron (NTM 1399, 1424-6, 1441-5, 1453-4, 1884-9), 17 mi. SE of Aileron (WAM 24426), Hermannsburg (NTM 2357-8, 2397-2402, 2607, 2635), near Reedy Creek, George Gill Range (NTM 1921-3, 1992-7, 2347), plus 48 specimens in the collection of the British Combined Services Expedition from Mt Olga, Armstrong Creek, Shaw Creek, Bonython Range, Davenport Hills, Kintore Range and Willie Rockhole (23° 16' S, 129° 45' E). *South Australia:* Musgrave Park (SAM 7170-7208), Itari Rocks (SAM 7598-7604), Mt. Davies (SAM 5311, 8411-14).

Egernia kintorei

Egernia kintorei Stirling & Zietz 1893, Trans. Roy. Soc. S. Aust. 16: 171. Lectotype locality: 60 mi. S of Barrow Range, Western Australia, in 27° 01' S, 126° 56' E (Elder Expedition).

Egernia dahlui Boulenger 1896, Ann. Mag. Nat. Hist. (6) 18: 233. Roebuck Bay, Western Australia (K. Dahl).

Diagnosis.—An extremely large member of the *E. whitei* species-group with short thick appendages, short deep head, pale reddish-brown dorsum and grey sides. Most like *E. striata* from which it can be distinguished by its much greater size, more numerous midbody scales, labials, presuboculars and upper palpebrals, short rectangular ear lobules, and much wider pupil.

Distribution.—Great Sandy, Gibson and Great Victoria Deserts of Western Australia, and the Tanami Desert of Northern Territory.

Description.—Body stout, not depressed. Ear aperture narrow; lobules 4-6 (mostly 5), small, subequal, their free edge usually truncate and thus parallel to margin of aperture. Snout-vent length (mm): 75-206; smallest male with everted hemipenes 161. Length of appendages (% SVL): foreleg 23-33, hindleg 27-41, tail 92-130.

Nasals widely separated; groove representing nasal-postnasal suture usually discernible. Prefrontals forming a median suture (seldom separated). Frontal a little wider or narrower than interparietal. Loreals normally 2, second 1.5-2.2 times as high as wide except when transversely divided (10% of specimens). Presuboculars usually 3. Supraciliaries 7-10 (mostly 8 or 9). Upper palpebrals 12-17 (mostly 13 or 14). Upper labials 7-9 (mostly 8, rarely 7), third-last usually precluded from orbit by enlarged palpebrals. Midbody scales smooth in juveniles, dorsally striate or feebly tricarinate in adults; 43-52 rows. Lamellae under fourth toe 17-23, entire or proximally divided, smooth or weakly callose, sometimes fusing medianly.

Back pale reddish-brown with faint or moderately strong longitudinal stripes caused by darkening of lateral edges of scales. Sides grey, the colour tending to concentrate in broad indistinct vertical bars curving forwards inferiorly; bars separated by narrow zones in which odd scales are posteriorly edged with greyish white; sometimes grey is disposed as a coarse reticulum. Upper surface of limbs reddish-brown diffused with grey. Eyelids pale brown, their free edges margined with creamy white. Labials whitish, sometimes the posterior narrowly margined with pale brown. Under surface yellowish white.

Remarks.—In spite of its extreme size and northwestern locality, the type of *dahlia* undoubtedly belongs here, as Loveridge (1934: 337) suggested and Mitchell (1950:284) confirmed when designating a lectotype for *kintorei*.

Material.—*Western Australia*: Kimberley Division—Sturt Creek (WAM 4007-8); Eastern Division—near Godfrey's Tank, Canning Stock Route (WAM 4002, 4004-6), near Warburton Range (WAM 22117, 22177), Kathleen Valley (WAM 27228), 24 mi. ENE of Laverton (EP 16912), *Northern Territory*: Tanami Desert Sanctuary, 20° 12'-16'S, 130° 30'-59'E (NTM 2087-8, 2321, 2612, 2618-28, 2640-9), 20 mi. E of The Granites (WAM 28602-13).

Discussion

The most debatable part of the foregoing classification is the treatment of the *Egernia whitei* superspecies. I have been reluctant to combine all these more or less dark and depressed skinks into one species merely because they are allopatric. In many respects *E. whitei tenebrosa* is more like *E. multiscutata* than it is to *E. pulchra* and other members of the superspecies; yet *tenebrosa* and *multiscutata* are sympatric at Birchmore Lagoon, Kangaroo Island. Again, the differences between *whitei* and *margaretae* seem to be of a higher order than those between such sympatric species as *slateri* and *inornata* or *striata* and *kintorei*.

It is by no means certain that *whitei*, *tenebrosa* and *modesta* are only subspecifically distinct. I have combined them into a single semi-species because of their adjacent ranges and similarly coloured juveniles. However nominate *whitei* comes within 12 miles of the range of *tenebrosa* without showing intergradation. The southernmost locality of *modesta* is only 75 miles north of the range of *tenebrosa*, but very few of the sharp north-south clines observed in *tenebrosa* extend to *modesta*.

It is still more doubtful whether *personata* and *margaretae* are races of a single semi-species. Few of the marked differences between them could have been predicted from the difference in latitude of their ranges or from the closer proximity of *personata* to *whitei tenebrosa*. The principal characters that unite *margaretae* and *personata* (strongly callose digits, tuberculate pads and degeneration of colour pattern) could have evolved independently in response to similar environments (rocks in semiarid mountain ranges).

At present there are only two members of the *E. whitei* superspecies that are certainly conspecific, namely the two races of *E. pulchra*. Finality on the status of the other members of the superspecies awaits material from critical localities and will probably require the consideration of more characters than were studied in the present work.

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Obituary—Professor A. D. Ross

On December, 14, 1966, at Albany, Western Australia, Professor Alexander David Ross died, peacefully after a short illness, at the age of 83.

Born in Glasgow in 1883, Professor Ross had a distinguished career at the University of Glasgow, where in 1905 he was Thompson Research Fellow. In 1906 as Houldsworth Research Fellow he studied at the University of Gottingen, and in 1908 was appointed Lecturer in Natural Philosophy at the University of Glasgow. His research interests were in the fields of magnetism and spectroscopy. In recognition of his researches the University of Glasgow in 1914 awarded him the Kelvin Medal, of which he was the first recipient.

Upon the foundation of the University of Western Australia, Professor Ross was appointed in 1912 to the Chair of Mathematics and Physics. He arrived in Perth to take up duties early in 1913. In that year classes commenced. When in 1929 Mathematics and Physics were separated he took over the Chair of Physics until his retirement in 1952. Except for a visit to Europe during World War I and again in 1951, Professor Ross gave uninterrupted service as teacher,

scientific investigator and consultant, and administrator over a period of nearly 40 years. He was the last in office of the eight foundation Professors. By his students he will be remembered, particularly as a teacher, clear in exposition, thorough in treatment, and considerate to all who were zealous in their aspiration to academic distinction.

Professor Ross played a distinguished part in building up the University tradition in the State of Western Australia as Professor of Mathematics and Professor of Physics, and in the numerous posts he has held in scientific and other organisations within and without the University. He and other Professors, coming from abroad in the early days of Australian Universities, had the distinction of being agents for the transmission of higher educational standards and sound cultural traditions to the State of Western Australia.

In addition to his services to many other organisations within and beyond Western Australia Professor Ross served on the Council of the Royal Society during 1930-31 and 1939-1942, and was President for three terms—1923-24, 1924-25 and 1940-41.

Errata—Membership List

It is regretted that two categories of membership were omitted from the Membership List of the Society published in Part 1 of Volume 50 of the Society's Journal. These should have been included as shown:—

Honorary Associate Members

H. P. Rowledge 52 Labouchere Road, South Perth.

Miss K. M. Shelton Flat H8, Hollywood Village, Williams Road, Nedlands.

Life Members

S. W. Carey Geology Department, University of Tasmania, Hobart, Tas.

Mr. Rowledge was inadvertently omitted from the published list altogether, while Miss Shelton was wrongly shown as both an Ordinary and Associate Member. Professor Carey, the only Life Member of the Society, was shown as an Ordinary Member.

INSTRUCTIONS TO AUTHORS

Contributions to this Journal should be sent to *The Honorary Secretary, Royal Society of Western Australia, Western Australian Museum, Perth*. Papers are received only from, or by communication through, Members of the Society. The Council decides whether any contribution will be accepted for publication. All papers accepted must be read either in full or in abstract or be tabled at an ordinary meeting before publication.

Papers should be accompanied by a table of contents, on a separate sheet, showing clearly the status of all headings; this will not necessarily be published. Authors should maintain a proper balance between length and substance, and papers longer than 10,000 words would need to be of exceptional importance to be considered for publication. The Abstract (which will probably be read more than any other part of the paper) should not be an expanded title, but should include the main substance of the paper in a condensed form.

Typescripts should be double-spaced on opaque white foolscap paper; the original and one carbon copy should be sent. All Tables, and captions for Figures, should be on separate sheets. To avoid unnecessary handling of the original illustrations authors are requested to include additional prints, preferably reduced to the final size required; a choice of either one-column (about 2.8 inches) or two-column (about 5.8 inches) width is available. The preferred positions of Figures should be marked on the second typescript copy.

In the preparation of references, and for all matters of presentation not otherwise covered in these instructions, authors are required to follow the *C.S.I.R.O. Guide to Authors* (Melbourne, 1963). Failure to read through this carefully before preparing papers may lead to delay in publication. The use of the various conventional systems of nomenclature recommended in this booklet, and in the supplementary pamphlets referred to in it, is obligatory; for this purpose, palaeontological papers must follow the appropriate recommendations for zoology or botany. All new stratigraphic names must have been previously approved by the Stratigraphic Nomenclature Committee of the Geological Society of Australia.

Thirty reprints are supplied free of charge. Further reprints may be ordered at cost, provided that orders are submitted when the galley proofs are returned.

Authors are solely responsible for the accuracy of all information in their papers, and for any opinion they express.

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Editor: A. F. Trendall

Assistant Editor: W. A. Loneragan.

The Royal Society of Western Australia, Western Australian Museum, Perth